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THE UNIVERSITY OF ALBERTA

The Analysis of a Predatory Interaction Between *Didinium* and *Paramecium*

by

© Brendan G. Veilleux

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "The Analysis of a Predatory Interaction between Didinium and Paramecium" submitted by Brendan G. Veilleux in partial fulfilment of the requirements for the degree of Master of Science.

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Abstract

The interaction between the predator Didinium nasutum and its prey Paramecium aurelia was studied in the laboratory and analyzed. The addition of Methyl Cellulose to the medium in which the interaction occurred prolonged the coexistance of the species in the microcosm. The results were used to construct vector maps and the zones of attraction in the phase plane in order to determine the positions of the zero isoclines of the interacting species. Rosenzweig and MacAruthur's (1963) graphical model of predation was applied to the system and was shown to be valid with few modifications. These included the use of predator time-lags and limit cycles to describ the behavior of a system.

By controlling the conditions of the environment, both abiotic and biotic, the interaction could be made stable or unstable at will. The correlation between the abiotic influences on the system with the biological parameters of the species and the stability of the interaction were interpretated. General conditions for stability in predator-prey systems were discussed in terms of both the biological characteristics of the species and the graphical theory. The searching rate of Didinium is a predominant factor in determining the outcome of the interaction. Under certain conditions however, other factors such as the predatory success rate, assume paramount importance in

governing the dynamics of the system.

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Introduction

One of the basic challenges facing modern ecology is to understand and predict the dynamics of natural populations. Since the theoretical works of Lokta (1920, 1925) and Volterra, a plethor of models describing the dynamics and temporal patterns of animal populations have been conceived. It is unfortunate, however, that supporting evidence, either experimental or observational, for many of these models has not been quite as prolific. The dynamics of interacting systems have been generally described in terms of time invariate differential equations (see May, 1974) or difference equations. The earliest models described the dynamics of a system in terms of a few species in total biotic and abiotic isolation. The environment was assumed invariable and usually optimal. More recent theoretical studies have begun to emphasize the importance of the abiotic environment and other cohabitants of the system (Engstrom-Heg, 1970; Pretwell, 1972; Leslie and Gower, 1960; Levins, 1968; Oaten and Murdoch, 1975; Oster and Takahaski, 1974; Murdoch and Marks, 1973; Rosenzweig, 1973a; Smith and Mead, 1974).

Between any pair of species there are two main types of interactions that can occur. These are competition and predation; the latter interaction is the focus of this study. When studying the predatory interaction, we are most

interested in the behavior of the system around the equilibrium point and the chances and causes of extinction for one or the other of the two species.

The relative complexity in the interpretation and integration of the causal factors influencing the dynamics of even simple predator-prey systems has resulted in many investigators turning from the study of such systems. They have instead, focused their attention on the behavioral and physiological aspects of predators (Holling, 1965, 1966; Salt, 1967). As Maly (1969:60) states, "these studies have contributed to an understanding of many factors that affect the dynamics without contributing substantially to a knowledge of the dynamics themselves." Many of these studies are predominately qualitative in nature and non-dynamical in interpretation.

Rosenzweig and MacArthur (1963) derived a graphical model for the theory of predation that greatly simplifies the interpretation of the dynamics occurring in the systems. However, because of the scarcity of observational evidence supporting this theory, its practical application to biological systems has been limited.

The system composed of the two ciliates Didinium nasutum and Paramecium aurelia is quite unique. It probably represents one of the closest approximations that a natural system can attain to the conditions defined by the classical predation theories (Tanner, 1975.)

The classical models in their strictest or simplest sense, demand that (Smith and Slatkin, 1973; Smith, 1972)

(1) in the absence of predation, the growth of the prey population follows the logistic equation or at least some form of self-limitation.

(2) the rate at which predators consume the prey is proportional to the product of the densities of the two species.

(3) the reproductive rate of both populations is continuous and dependent upon the rate of food intake.

The most serious failure of the Didinium - Paramecium system to conform to the above is a result of the assumption implicit in (3); the assumed absence of time-lags between the component populations.

The purpose of this study was to investigate the predator-prey interaction using the Paramecium - Didinium system. The aims of this work were;

(1) to determine the usefulness of the graphical theory of predation, basically by the construction and manipulation of the isoclines of the system, and the comparison of the isoclines derived under different sets of abiotic conditions.

(2) to analyse the predation process with respect

to the characteristics of the predator and the prey.

The Didinium - Paramecium system is what might be called a 'biological' model, basically just a laboratory ecosystem. Such devices are a useful bridge between the theoretical models and simulations, and real ecosystems. As Smith (1974:3) states " Their main value has been not so much in checking the deductions made from mathematical models but in suggesting phenomena that the mathematicians should be able to explain. ... Mathematical and biological models complement one another; in the absence of biological models, the mathematical treatment would tend to become more abstract and general, and to that extent more difficult to apply. In the absence of mathematical treatment, it would be difficult to see the general relevance of particular biological variables".

The study of the dynamics of the Didinium - Paramecium system was sparked by Luckinbill's (1973) success at developing an experimental techinque allowing the prolonged laboratory coexistence of mixed populations of this predator and prey. The method is unique in that it is without the complicating spatial heterogeniety that characterizes other systems (see Huffaker, 1958; Huffaker et al., 1963). With these techinques, the interaction between the predator and the prey can be studied with the least amount of external influence. By controlling the experimental milieu of the

system, the factors of major importance in determining the outcome of the interaction can be ellucidated.

Luckinbill found that prolonged coexistance of interacting populations of Didinium and Paramecium could be achieved by a combination of two experimental conditions:

(1) limiting the food supply to the prey and
(2) reducing the frequency of contact between the predator and prey.

The latter condition is accomplished by the addition of the highly cross-linked polymer Methyl Cellulose to the medium. Methyl Cellulose is commonly used to decrease the velocity of protozoans and it achieves this effect by increasing the viscosity of the medium. Methyl Cellulose acts in no way as a physical barrier but has distinct effects on the dispersal rates of the predator and prey. This polymer has no direct physiological effects on the animals in terms of toxicity (Luckinbill, 1973).

The basic design of the experiments performed in this study relies on the combination of two factors; varying concentrations of Cerophyl in the medium (a bacterial nutrient) associated with the presence (or absence) of Methyl Cellulose. Varying the concentrations of Cerophyl produces differing degrees of Paramecium 'starvation'. This has implications in the continued coexistence of the interaction between the species in a mixed culture. The

carrying capacity of the Paramecium, and, as a consquence, their nutritive condition, is directly related to the bacterial density in the medium (see Canale et al., 1973). The bacterial density is a linear function of the Cerophyl concentration, and therefore, the nutritive state of the prey can be considered as a direct function of the amount of Cerophyl in the medium.

Because of the relative simplicity of the characteristic responses of the animals used in this study, the dynamic forces acting on the populations can be understood. The biological parameters involved in directing these forces, and the determination of the orientation and positioning of the isoclines of the component species may also be obtained. What is the value of such knowledge? If for no other reason, as Luckinbill (1973:1320) states, "it is important that a firm experimental basis be established for the existing theories of predator-prey interactions".

In addition to the above, an understanding of the dynamical interactions of predator-prey systems leads to a predictive ability for community evolution and a manipulative techingue that has implications in pest control, resource management, harvesting techinques, enrichment phemcnenon, and so on (see Beddington, 1975; Bigger, 1973; Hassel, 1969; Hassel and Varely, 1969; Watt, 1968; Debach, 1972; Huffaker, 1974; Rosenzweig, 1971). In a more immediately practical vein, it is well known that the

activity of protozoan predators in biological waste treatments operations reduces the density of the prey populations with a resultant decrease in the rate of stabilization of waste effulents. Canale et al. (1973) describes in detail the effects of such microbial predators on the efficiency of engineering systems concerned with space life support.

The Graphical Theory

The basic theory of the predator-prey interaction remained more or less unchanged with respect to the Lokta-Volterra interpretation (though the models became considerably more complex, see Leslie and Gower, 1960) until the advent of Rosenzweig and MacArthur's graphical model of dynamic predator-prey systems. Rosenzweig and MacArthur (1963) presented a theory of predation which arose as a result of investigations into the problem of over-exploitation in predator-prey systems. This is a rather specialized aspect of a much more encompassing problem, the study of the mutual behavior of two or more variables which are connected by a series of differential equations (see Davis, 1963). If cyclic variations in one of the variables causes cycle variations in the other, there may be a hystersis or time-lag in the relationship between them. This has direct implications in the descriptions of predator-prey systems. The periodic oscillations of predatory systems owe their existence, to a large extent, to the inherent time-lags in the predator and prey responses to changes of their own and each other's density. Since the studies of Volterra, a method borrowed from classical physics to study the nature of coupled oscillations has been used in the study of exploitative dynamics (Davis, 1963). The trajectory of a predator-prey system is plotted in the confines of a graph having for its two axes the predator (ordinate) and the prey (abscissa) densities respectively. This plot is

known as the phase space (or plane) and can be used to determine the behavior of a coupled system.

Rosenzweig and MacArthur envisaged the plane of the phase space as a set of points in a vector or direction field (a collection of line segements following some predetermined solution set for the plane; biologically, this represents the changes in numerical density of the interacting population take in the phase plane). Rosenzweig and MacArthur used this concept to determine graphically the oscillatory behavior and eventual outcome of predator-prey systems given certain component characteristics. Each ordered pair in the phase-plane is considered to represent a unique composition of predator-prey densities. With each of these points is associated a unique pair of orthogonal vectors. These vectors (or their resultant) indicate the direction of the instantaneous rate of change of the predator and prey populations at any given community composition.

There are three biological assumptions explicit in this representation (Tanner, 1975);

(1) there are no third species interactions, this includes the conditions that;

(a) the predator mortality rate, due to causes not associated with prey density, is constant.

(b) the predator feeds only on the prey.

(c) though the prey food supply is limited, it is

never overexploitated.

(2) there are no time-lags in the respones of either the predators or the prey to changing conditions.

(3) the two populations live in the same area so the density of these populations is proportional to their number.

The phase plane is divided into four quadrants by two curves known respectively as the predator and prey zero isoclines (or just isoclines). These curves represent all the points where the rates of change in each population become zero. From the position of these isoclines the dynamical characteristics of the system can be determined (see Canale, 1970; Freedman, 1976; Gilpin, 1972; Goel and Strebel, 1973; Goh et. al., 1974). Armstrong (1975:3) has derived an alternative graphical theory that does not require a knowledge of the positions of the zero isoclines but involves rather "a direct consideration of the prey's productivity curve and the predator's fuctional response curve". This is a more analytic elaboration of Rosenzweig's (1969) work.

The graphical theory predicts that the coexistance of the component species in a predatory interaction is determined by the relative positions and intersections of their respective isoclines. If the predator isocline lies to the right of the 'hump' (Rosenzweig, 1969) (the maximum of

this curve with respect to the predator axis) in the prey isocline, the interaction (equilibrium) is stable. All trajectories of the system spiral inwards toward the equilibrium point (an exception to this interpretation which is quite important in the dynamics of many systems will be mentioned later). Biologically, this situation represents an inefficient predator, one that can only exploit the prey effectively at relatively high prey densities.

When the predator isocline intersects the prey curve at, or in the near vicinity of the hump, oscillations of constant amplitude about the equilibrium point result. Here the predator is effective at exploitating the prey at their intermediate densities.

In those cases where the intersection of the predator and prey isoclines lies to the left of the hump, the trajectories of the systems spiral outwards, away from the equilibrium point and will eventually contact one of the axes. This case is represented biologically, by an efficient predator capable of utilizing and exploitating prey even at low prey densities (MacArthur and Connell, 1966). Gilpin (1972) has shown that with this case, the trajectories need not neccessarily intersect the axes but may form a stable limit cycle. However, the trajectories approach the axes so closely that this situation becomes biologically unrealistic. In this study it was shown that the outcome of the interaction may become a function not of the component

populations, but of the external milieu when the populations drop below 3 individuals per ml.

The dynamics of a two species predator-prey system can be given by

$$dx/dt=xf(x,y)$$

$$dy/dt=yg(x,y)$$

This system has singular points at the orgin; where the prey isocline intersects with the prey axis; and where the predator and prey isoclines cross. There are no equilibrium points on the predator axis since this would require the predator isocline to come in contact with it. Such an intersection would imply social facilitation in the predator population to such a degree that the predators could increase in the absence of the prey. It could also imply that the predator feeds on an alternative resource if the interaction was greater than two-dimensional. All predator-prey systems of the form described above, have, as stated by May (1974:75), "a tension between a stabilizing resource limitation or other density-dependent terms, and destabilizing predator functional and numerical response terms". It was generally assumed that when a system was analyzed, if no stable equilibrium point was found, the system was unstable (May, 1974). However, it was shown by Kolmogorov (in May, 1974; Rescigno and Richardson, 1967; Scudo, 1971) and recently proved by Albrecht et al. (1975), that a system may have either a stable equilibrium point or

a stable limit cycle provided (f) and (g) are continuous functions of x and y and certain conditions hold (see May, 1974)

The nature of an equilibrium point is dependent both on which side of the hump it lies and on the characteristics of the system. The Rosenzweig and MacArthur model holds only for vertical predator isoclines or, in the case where this isocline is tilted or curved to the right, as long as its intersection with the prey axis is to the right of the hump. It the predators isocline is not vertical and intersects the prey axis to the left of the hump, no definite statement can be made about the nature of the equilibrium point (Gilpin, 1974).

Though a number of theoretical studies have had their basis in the graphical predation theory, little experimental support for the model has been forthcoming. Rosenzweig (1969) attempted to validate the theory by analysing the results of Huffaker (1958) and interpretating them in terms of the graphical model. This work, however, has been critized by Goel and Strebel (1972), their main concern being with the failure of the data to conform to three basic assumptions explicit in the graphical interpretation. These conditions are as follows;

(1) the environent must be more or less constant, otherwise the system can no longer be

interpretated as a simple two species interaction; in effect, a deterministic event is replaced by a more complex stochastic one with other unknown factors included.

(2) every point in the phase plane has a unique vector associated with it and each point itself is unique. If this condition does not hold the biological implication is that the intrinsic rate of increase of the populations can change independently of the environmental forces or population density, and the system is governed by its past history. Though this type of variation in the growth rate is not biologically impossible, it makes the analysis of the system's dynamics unpleasantly complicated. This condition also assumes that populations of identical density components do not vary in any other respects of their parameter space (see May, 1974).

(3) the growth of the population is continuous. As stated by Rosenzweig and MacArthur (1963:74), "in a continuous model, a population cannot pass from an increasing state to a decreasing one or visa versa, without attaining an equilibrium point (dx/dt=0) en route".

Maly (1969) presented some evidence supporting the graphical theory with a system composed of the predatory rotifer Asplanchia brightwelli, and the prey Paramecium

aurelia. He experimentally determined the population vectors of the system, indicated the presence of the isoclines, and demonstrated that the predictions of the graphical model were consistent with the observed dynamics. There may be some difficulity with the way these vectors were determined, however, and this will be dealt with later.

The results of Canale et al. (1973) on the consumption of the bacteria Aerobactor aerogenes by the protozoan Tetrahymena pyriformis show that the behavior of a predator-prey system can be accurately predicted by the graphical method. Goel and Strebel (1972) analysing Huffaker's (1958, Huffaker et al., 1963)) data by the grahpical method find that the the shapes of the actual isoclines are not overly regular, and that the prey isocline is not concave or flattened as expected. They also find that a stable system is forming (damped oscillations) even though the intersection of the isoclines is to the left of the 'hump' (Rosenzweig, 1969) in the prey isocline. This latter point is somewhat of a contradiction of the grahical theory as expounded by its authors. It may be that the graphical theory in its more general form, may only be of value for simple natural systems. It was the hope, in part, of this present study to illuminate some of the values and faults in this theory.

The Experimental System

Though protozoans are considered unicellular (a rather inadequate description), as Hyman (in Keeton, 1967:842) has pointed out "each protozoan is to be regarded not as equilivant to a cell of a more complex animal, but as a complete organism with the same properties and characteristics as cellular animals". Due to the relative simplicity of the protozoan behavioral response and life cycle, any features of biological interactions basic to all animals in general should be present in this group, uncomplicated by the pecularities of a more advanced nervous system (see Holling, 1959, 1965).

The protozoans used in this study are identical to those used by Gause (1934). The Holotrichous ciliate Paramecium aurelia served as the prey for the predatory Rhabdophorine ciliate Didinium nasutum. The resource for the prey was the bacterium Aerobactor aerogenes. Paramecium aurelia is a relatively large ellipsoidal protozoan (140 microns, Jurand and Selman, 1969). For a morphological description of this animal see Corliss (1961) or Jahn and Jahn (1949).

Didinium nasutum is a barrel-shaped predator with a short cone-like projection (or proboscis) protruding from the centre of a flattened anterior region. The conical proboscis constitutes the feeding apparatus, whose action is governed by means of two distinct types of trichocysts. A

description of this structure along with Didinium's feeding behavior is covered by Wessenberg and Antipa (1968, 1970).

Didinium does not actively pursue prey in the sense of 'chasing' them, nor do they seem to recognize the physical presence of the Paramecium. Contact with a prey is a result of purely random collision (Jennings, 1931; Manwell, 1968; Wessenberg and Antipa, 1970). There is no chemoattraction of the predator to the prey; as Wessenberg and Antipa (1970:64) state, "if a chemotaxis is involved, it is more likely due to the same environmental zone".

In the absence of predators, Paramecium increase in a logistic manner with a slight initial over shoot of the carrying capacity (Gill, 1972a, b; Leslie, 1957; Vandermeer, 1969). When Didinium is supplied with sufficient prey, they increase initially in an exponential manner, however their final density is directly dependent upon the density of the prey.

The functional response curve of Didinium is characterized by a negatively accelerated rise to a plateau. This is an example of the Holling Type II curve, typical of many invertebrate predators (Holling, 1959, 1965; Rashevsky, 1959). The mathematical analysis of this protozoan system is greatly simplified since age specific birth and death rates, and population age structure can be neglected. An example of this can be seen in the work of Leslie (1957).

This protozoan system has a number of other convenient properties that make it easy to deal with, both logistically and conceptually;

(1) this system requires little space, an entire dynamical event can occur in a drop of water.

(2) many replications of a given experiment can be obtained in a short period of time, both as a result of the organisms short generation time and the simplicity of the experimental system.

(3) the reproductive rate in terms of the number of progeny per generation of both species is exactly two.

(4) under properly maintained conditions there are no sexual or larval stages to deal with.

(5) animals in the process of reproduction or digestion are obvious.

(6) protozoans are quite tolerant to oxygen depletion and varying amounts of metabolites; therefore the dynamics of the interaction are not overly influenced by these factors if some care is taken to renew the experimental medium (Noland and Gojdines, 1967).

(7) there is no interference competition within the populations of the species used in this study.

(8) the density of the prey species in a given environment is a linear function of the food

concentration (Canale et al., 1973; Hall, 1967).

(9) the biology of the animals is extremely well known and this has resulted in the development of reliable and standardized culture techinques (Chen, 1967; Corliss, 1961; Curtiss, 1968; Calkins and Summers, 1964; Hall, 1967; Kudo, 1966; Jones, 1974; Sonneborn, 1950; Wichterman, 1953).

The Feeding Biology of *Didinium*

Dininium nasutum was first described by O.F. Muller (1786) (in Manwell, 1968) and it feeding behavior has since been described by Stein (1859), Balbiani (1873), Thom (1905) and Mast (1909) to name a few. The most recent studies have tended towards morphological descriptions (Faure-Frement, 1959; Wessenberg and Antipa, 1968, 1969).

Didinium is a voracious predator with a distinct preference for species of the genus *Paramecium*, though it will take *Colpoda*, *Colpidium*, *Vorticella*, *Frontonia*, and even flagellates under extreme conditions (Mast, 1909; Beers, 1937). It is thought, however, that only a diet of *Paramecium* is completely adequate for its continued reproduction (Manwell, 1968).

Didinium can consume enormous quantities of prey. In the words of Mast (1909:112), "if they should take a *Paramecium*, averaging one and a half times their own size, every three hours, in twenty-four hours they would consume a mass of substance having a volume twelve times as great as their own. I know of no other creatures that even approach these in their feeding capacity". A given *Didinium* and its subsquent descendants can consume, under ideal conditions, at least 45 paramecia per day. Because of this ability to efficiently utilize prey, it is significant that *Didinium*

has evolved encysting mechanisms allowing them to survive times of prey shortage.

Didinium is a unique predator with a highly developed means of capturing prey. Didinium swim rapidly, rotating on their longitudinal axis and spiralling slightly along the line of motion. In the Cerophyl medium, Didinium turn frequently and, at the vertices of each turn, make a number of short jabbing motions in all directions. This hunting behavior has been described by Mast (1909:96) " if a number of didinia are studied under a lens, they appear to be darting about in the wildest confusion, sharply turning to the right and left, up and down, and frequently running into one another. ... In thus rapidly swimming about, they cover a large space in a short time and come in contact with everything that may happen to be in this space". Calkins (1915:7) similiarly describes this behavior.

When a Didinium swims into a Paramecium in such a manner that its proboscis contacts the prey, there is an immediate discharge of its trichocysts into the prey (see Wessenberg and Antipa, 1968). Two types of trichocysts are involved; Toxicysts, which produce a toxin that severely disables the prey; and Pericysts that act as a trigger for the toxicysts. The entire capture and ingestion process takes about a minute, after which time the Didinium touches its proboscis to the substrate and slowly rotates for two hours. Of this period, only 20 to 30 minutes are involved in

the digestion of the prey, the rest of the time is occuppied in resynthezing the feeding apparatus (Manwell, 1968).

Didinium has a rather unique means of digestion. The Paramecium supplies not only nutrients to the predator, but also the enzyme required for its own digestion, a dipeptidase (Dolye and Patterson, 1942). Possibly this is why Didinium is an obligate predator of Paramecium. It is also possible that Didinium is dependent upon Paramecium because of the prey's physical size. The hunting behavior of Didinium requires lavish expenditures of energy. The process of resynthezing the feeding apparatus is also costly in terms of energy consumption. As a result of these drains on the predators internal resources, and in addition, due to the limitation imposed upon the feeding rate by the resting phase, Didinium must maximize its net energy input at each capture. It may be that only large prey, like Paramecium, are capable of supplying the predator with sufficient energy resources. Though Didinium does consume other prey species, all of them are considerably smaller than Paramecium and are taken only when the predators are desperately starved.

The physiological state of Didinium is dependent upon the nutritive condition of the prey (Beers, 1928; Burbanck and Eisen, 1960; Butzel and Bolten, 1968). Didinium, feeding upon starved prey, are characterized by decreased fission rates, cell abnormalities and the loss of the ability to encyst. All of these features were observed in this study.

Methods and Materials

The prey species used in this study, Paramecium aurelia (syngen 4.stock 51S, mating type VII), was kindly supplied by G.W.Salt. The predator, Didinium nasutum was kindly supplied by J. Addicot.

The P. aurelia were grown in Cerophyl medium following the methods of Sonneborn (1950) and Wichterman (1953). The medium is very satisfactory for experimental work where rapid and uniform reproductive rates of the protozoan populations are required. Cerophyl acts as a bacterial nutrient and supports the vigorous bacterial populations upon which the Paramecium feed. The Cerophyl used throughout the study came from the same batch. The suitability of all media for experimental use was tested by means of the serial transfer techinque described by Sonneborn (1950).

Most of the data obtained from the various experiments were non-normally distributed. This was determined by applying a graphic procedure to the data, the ranked normal deviate method (Sokal and Rohlf, 1969), which examines the shape of an observed distribution for departure from normality. Since the data do not in general meet the assumptions required for the analysis of variance and other parametric tests, non-parametric methods were used. Since most of the comparision of data groups is between two classes, the Mann-Whitney U test was used to determine the significance of the difference between these classes. An

analysis of variance was applied to the data concerning the population oscillations and perturbations since these were normally distributed.

Unless otherwise noted, all experiments were run at 27°C in 15mm X 60mm petri dishes (standard culture vessels), containing 6ml of medium. To simplify the description of the various experimental media conditions, the abbreviation 'CCn' will be used to represent the precise Cerophyl concentration of the medium where n represents the concentration. For example, CC0.75 represents three-quarters strength Cerophyl. Those systems containing Methyl Cellulose will be represented by 'MC' and those not containing the polymer by 'NMC". The nutrient concentrations used in this study are based on and are proportional to CC1.0, defined at a Cerophyl concentration of 1.8 grams per liter. Thus, the Cerophyl concentration of say CC0.5 is 0.9 grams per liter while that of CC0.375 is 0.68 grams per liter and so on.

During the preparation of the medium, sterile techniques were maintained until just before use since, as Sonneborn (1950:95) states, "at this stage the single strain of inoculated bacteria has nearly or quite exhausted the nutriment and this inhibits appreciable growth of most bacteria which can come in as contaminants". The pH of the medium was adjusted to 6.7-6.8 since this is optimal for both protozoan populations used in this study (Koffman, 1924).

The *Didinium* were stored in the encysted form. Since these cysts are unable to withstand dehydration, they were continually stored in a modified Knop solution (Beers, 1937).

To assure sterile populations, the animals used in an experimental system were washed beforehand five times in sterile media (Salt, 1967). If outside contamination of the cultures was thought to have occurred, the animals were sterilized by the methods of Hetherington (1934) (also see Parpart, 1928; Trager, 1937 for simpler approaches).

The preparation of the Methly Cellulose medium was accomplished following Luckinbill (1973). Care was taken to assure the complete dissolution of the Methyl Cellulose. This requires prolonged (about 30 minutes) stirring of the bacterized medium at room temperature. This procedure did not however, appear to have any effect on the quality of the medium. The growth rates of *Paramecium* in stirred and unstirred NMC systems were compared and no significant difference between the groups was found ($U=22$, $0.25<P<0.50$, $n1=24$, $n2=30$).

Sampling methods

To determine the population densities, the systems were sampled non-destructively. Before sampling, each system was thoroughly mixed; immediately after mixing, a 0.1 ml sample was removed from the culture, the number of animals in it

counted (by a Wild M3 dissecting microscope, 16X), and the animals returned to the system. For each system, eight such samples were taken and the number of individuals per ml found from the mean of these results. Eight samples were taken since it was found that this number gave the greatest accuracy for the time involved.

The errors involved with this method are presented in Table 1. The average sampling error was about 3.5 percent. The greatest errors in the approximations of population size occurred at relatively low densities, those of about 50 individuals or less per ml. At these densities (easily approximated at a glance) all the individuals in the system were counted and no sampling was performed. This procedure reduces the mean error in accuracy to about 2.5 percent.

Renewing the systems

In the long-term experiments (periods of over two days) it is neccessary to prevent the build-up of metabolic waste products and to keep the bacterial density in the cultures at a level conducive for maximum prey growth. To achieve this, one-half of the medium in each system was replaced by a similar amount of fresh bacterized Cerophyl every two days. The organisms present in the discarded portion were returned to the system. Approximately 1 ml of the total volume of the system was lost every 10 days due to evaporation. This quanity was regularly replaced with

sterile water.

Experimental procedures

The persistence of the interaction in these microcosms is a direct result of the concentration of Cerophyl in the medium. By measuring the various population parameters of the component species at different CC levels, significant trends in these factors can be correlated with the stability observed in any experimental system. The persistence or extinction of the systems can then be interpreted in absolute terms with respect to the biological parameters. An indication of which biological characteristics are most important in determining the outcome of the interaction can then be obtained.

The experiments performed during the course of this study can be grouped into three classes;

(A) Paramecium population parameters

(B) Didinium population parameters

(C) Population Dynamics of the Paramecium-Didinium system

These experiments will be described below.

A. Paramecium Population Parameters

Fission rates - Optimal

These experiments were performed to determine the differences in division rate between MC and NMC treatments and between the various CC levels within a treatment. This data, in combination with that obtained from the growth curves and carrying capacities can be used to quantify the effects of resource limitation on the prey population.

To find the maximum fission rate of the prey under a given set of conditions, Paramecium at the initial densities of 1, 3, and 5 individuals/ml were placed in 6ml of medium and left for 24 hours, afterwhich time the number of individuals present were counted. The number of divisions may be calculated by

(number of divisions) x ln(2) = ln(final total population density)

Growth Curves

Here the intraspecific action of the prey on their own population growth in the absence of predators was observed. This, as will be seen later, has important effects on the stability of the systems. An initial density of 15 individuals/ml was established in 6 ml of the appropriate medium. Replacement of the medium was carried out as specified. The populations were sampled every 12 hours, and the systems maintained until a stable plateau in density had been achieved for at least two days.

Similiar experiments were performed to determine the

carrying capacities of various CC systems. The chief difference between these experiments and those of the growth curves was the interval of sampling. The former runs were sampled only once a day beginning two days after the start of the experiment. The intrinsic rates of increase were calculated from the slope of the regression line derived from the growth curve data. The equation used for these calculations is $\ln((K-N)/N) = a - (rm)t$ where N is the population size; K is the carrying capacity; a is the y-intercept; t is time; and rm the the intrinsic rate of growth.

(B) *Didinium* Population Parameters

Fission Rates - Optimal

The effects of the prey at various nutritional states on the division rates of *Didinium* has been described previously by Beers (1928) among others. This feature was established quantitatively for this study. This parameter gives a numerical measure of the effects that the nutritional inadequacy of the prey imposes upon the predator reproductive output.

To find the maximum fission rate of *Didinium*, an individual predator was placed in one ml of medium saturated with *Paramecium* (approximately 500 individuals/ml) grown

under a given CC condition. The predators were starved 8-10 hours beforehand to assure that the divisions that did occur were not the immediate result of a previous feeding. The number of predators in the system after 24 hours was noted.

Predator Functional Responses

The feeding rate of the predator and its subsequent regulation by prey density and nutritional state was determined.

It is the functional response of the predator that makes them effective in controlling the prey. It describes the non-numerical response of the predator to increases in prey density. Rosenzweig (1969) and Armstrong (1975) have shown how the shape of the functional response curve influences the outcome of a mixed system. From this curve, a number of characteristics of the predator, both behavioral and physiological, can be determined (see later). Three initial densities of predators were used; 1, 2, and four individuals/system. Each experiment was run in 0.25ml of sterile medium. The feeding rate was calculated following Brobyn (in Sleigh, 1973). The number of Paramecium consumed in 24 hours is divided by the average number of Didinium present during this period. The Paramecium were starved before hand in the following manner; CC1.0 prey were starved 18 hours while the CC0.5 prey were not fed for 8 hours. It was found that no division occurred in the prey population

if Paramecium individuals were kept from food for these periods of time.

Number of Prey Required for Didinium Fission

This was performed between treatments at various CC levels to give an indication of the effects that prey resource limitation (in the form of starvation) has on the expected predator gross energy gain obtained from an attack on a prey. Assuming that a constant energy threshold is needed by Didinium for a division, this parameter also gives a direct measure of the degree of prey nutritional inadequacy at the differing CC levels.

Didinium were initially cultured on CC1.0 prey for two days prior to the actual experimental run. They were then starved 18 hours, after which time an individual was placed in 0.1cc of sterile culture medium containing 100 Paramecium grown at the desired nutrient condition. The Paramecium had been starved somewhat to prevent their division. Every two hours the systems were checked to see if a division had occurred. If a fission had occurred, the number of prey in the culture was counted. If one or both of the predators were in the resting phase, 1 or 2 respectively was added from the total number of Paramecium counted. This was done to account for the prey consumed by the predator after its fission.

Success of *Didinium* at Capturing Prey

The efficiency of *Didinium* at capturing *Paramecium* has direct implications in the dynamics of both the predator and the prey. This parameter can also be considered an indirect measure of the vitality of the predator.

A culture of *Didinium* was grown on the appropriate prey type for two days. Before the experiment each predator was starved for 6 hours. After this time, an individual didinia was placed in 0.1ml of culture medium with a prey density of at least 500/ml. The progress of the animal was observed. Success or failure at the first attempted capture was recorded, the animal discarded, and a new individual placed into the system. Success was considered as the capture and consumption of the prey.

Excystment of *Didinium*

This experiment had direct implications with respect to the evolution of *Didinium* since it involved the ability of the predator to perceive the quantitative and qualitative availability of the prey. Excystment of *Didinium* is a function of the bacterial concentration of the culture and not of the *Paramecium* density (Butzel and Bolten, 1968).

Six ml of Cerophyl medium, incubated for 36 hours, were placed in a petri dish. A known number of *Didinium* cysts

were placed into this vessel and after 18 hours, the number of non-excysted individuals was counted. Didinium is incapable of encysting directly after excysting without first feeding. Since no food was present for the excysted predators, any cysts remaining in the culture were those of non-excysted individuals. (Butzel and Bolten, 1963).

Estimate of the Rate of Prey Consumption Required for Predator Maintenance

These experiments, though crude, give an indication of the homeostatic energy costs in terms of prey biomass required by Didinium to survive. They can also be considered as a measure of the nutritional adequacy of the prey, and, when combined with the data from the prey/predator division experiments, they give a direct measure of the net amount of prey biomass needed to produce one predator.

One didinia was placed in 0.1ml of medium and fed a predetermined number of Paramecium per day. If, at the end of the 24 hours, any of the prey were still remaining, these were removed, and the initial prey density reestablished. The number of runs still containing predators after 7 days was recorded.

(C) Population Dynamics

Probability of System Extinction

This was performed to delimit those regions of the phase plane where the outcome of the interactions becomes strongly influenced by the environment.

Three different initial densities of Paramecium, placed in 6ml of culture medium, namely 1, 3, and 5 individuals/ml, were tested. Before the test, the prey were starved assuring no division immediately after the initialization of the experiment. The systems were left undisturbed and the number of surviving systems after 36 hours was observed. Every 8 hours the increase in the population was removed.

A similiar procedure was carried out for the predators. Prey, at a given nutrient condition, saturated the system (350individuals/ml).

Long Term Systems

It was with these experiments that the dynamical nature of the predator-prey interaction could be determined since here, the two species were allowed to interact with one another freely.

The initial densities of these systems were, unless noted otherwise, 15 Paramecium per ml and 5 Didinium per ml. The populations in these cultures were sampled every 12 hours and one-half of the medium was replaced every two

days. The cultures were allowed to run as long as they could, or at least until their behavior had been properly ascertained. It was found important not to disturb the systems any more than neccessary. Any non-random agitation of the cultures seemed to set up currents that tended to accumulate the animals at the centre of the culture vessel, which substantially increases the chances of a Didinium encountering a prey.

Perturbations of the Long-term Systems

The following experiments were performed to investigate the stability of the systems and to give better definition to the positions of the isoclines.

(i) Numerical Displacement

Once a system was oscillating with a constant amplitude, it was shifted to a new density by the removal or addition of one or both species. Protozoans to be added came from a synchronously running culture. Two cultures initiated at the same time and handled in the same manner were found to be synchronous with one another. Since the dynamics of the system depends so heavily upon the nutritive condition of the Didinium, individuals to be added must be in the same state as the predators already present in the system. Paramecium remain at a more or less constant nutritional state throughout a run since their food resources are more

or less constant.

(ii) Temperature Effects on System Behavior

When the systems were exhibiting stable oscillations, they were placed in a drying oven set at 60°C for 20 minutes. After this, the system was returned to normal conditions and allowed to run. Didinium can withstand maximium temperatures of about 52°C (Dingfelder, 1962). Paramecium are not as heat tolerant (Poljansky, 1963). The systems were not sampled and only their persistence or time to extinction was noted. The 'shock' occurred during the cycle just before the Paramecium reached their maximum density. This allows both the predator and the prey to be in the best relative condition to resist the temperature change.

(iii) Artifical Predation upon Didinium

This experiment and that immediately following (iv) were performed with the intention of determining whether or not the manipulation of the predator isocline by external forces was possible and, if so, what were the subsequent effects on the dynamics. The prey isoclines were manipulated by varying the CC level in the system.

Every 12 hours 25 percent of the total Didinium population was removed from the system, crudely simulating the action of a predator (Didinium-like). An attempt was

made to be non-selective in the predators removed.

(iv) Immigration of Didinium

Every 12 hours the total Didinium population in a system was counted and 25 percent of this number was removed from a synchronous culture and added. Again an attempt was made to be non-selective in the individuals chosen. The major problem encountered here was that the synchronous culture soon became out of phase with the experimental system owing to the disruption of the dynamics of both systems.

(v) Regions of Attraction

These experiments were preformed to determine the regions on stability and instability in the phase plane. Systems with extreme initial densities (other than the standard 15 prey / 5 predators per ml) were set up and allowed to run as usual. Only the persistence of these systems was noted.

Results

(A) Prey Population Parameters

Carrying Capacity

In both the MC and the NMC systems, the carrying capacity (K) decreases as a linear function of Cerophyl concentration. The linearity of K with respect to the nutrient concentration in the environment is not a new or unexpected phenomenon in protozoan systems (Hall, 1967; Luckinbill, 1973).

The carrying capacities of the prey at given CC levels were significantly lower in MC systems than in NMC cultures (Table 2a, b(stats), Figure 1). A simple linear regression was performed on the data and the following fits obtained;

NMC $K=-76.92+1.37x$, $r^2=0.98$, $n=55$

MC $K=-63.36+1.16x$, $r^2=0.97$, $n=88$

where x is the Cerophyl concentration. Assuming a linear response between bacterial nutrient concentrations and bacterial densities (Canale et al, 1973), these results indicate that given a specific density of bacteria, NMC systems support a greater population of the prey animal. This implies then that Paramecium living under MC conditions must expend relatively more energy in foraging for the resource than those in NMC systems. It is unlikely that Methyl Cellulose affects the initial density of bacteria in

a culture, since the procedure of adding Methyl Cellulose to the system does not seem to affect the bacterial population (see methods). Methyl Cellulose was added after the majority of the bacterial growth had occurred, as measured by the constancy of the pH of the media, therefore Methyl Cellulose would not be capable of inhibiting further large increases in bacterial density. It is unlikely that Methyl Cellulose actually causes an increase in the mortality rate of the bacterial population though this cannot be ignored.

Growth Curves of Paramecium

These curves follow the classical logistic form of population growth (Figures 2a-d). The rate of growth in the system decreases significantly with decreasing CC (Table 2a,c). A logarithmic regression of these values gives $3.25 + 1.371\ln(x)$, $r^2 = 0.96$, $n=55$. All systems initially overshoot K to a slight degree. However, they soon return approximately to it, oscillating with a small amplitude around it. This overshoot is not unusual in Paramecium populations (Gause, 1934; Vandermeer, 1969).

Fission Rates

The number of divisions per day in the Paramecium population is shown in Figure 3a. Not surprising, there is a good correlation between the divisions per day and CC levels (Table 3a,b(stats)). The regressions to these rates are;

NMC #paracecium/day=$36.01x^{1.18}$, $r^2=0.98$, n=98

MC #paramecium/day=$28.96x^{2.24}$, $r^2=0.96$, n=108

More importantly, at any given CC level, the division rates are always lower for MC systems than for the corresponding NMC systems. This is attributed to the increased maintenance costs of the animals in MC, less energy being availible for reproductive purposes.

The reproductive rates for the populations determined from these experiments do not compare favorably with those obtained from the growth curve runs, at least for the higher CC levels. The rm values obtained here are considerably higher than expected. These differences for CC1.0, CC0.75, CC0.50, CC0.375 and CC0.10 respectively, are 38 percent, 29 percent, 23 percent, 18 percent, and 6 percent. This can be attributed to in part to the differing initial densities of the experiments and the intraspecific competition within the prey population in the growth curve runs.

(B) Predator Population Parameters

Throughout this section for the purpose of simplification, the presentation of various predator parameters will be compared to the CC levels. It must be remembered that these characters are actually influenced by the nutritional state of the prey grown at these CC levels and not the levels themselves.

Fission Rates

As with Paramecium, the fission rate of Didinium drops significantly with decreasing CC levels and between NMC and MC systems (Table 3a, 3b, 3c(stats), Figure 4). The regressions to these curves are;

NMC #didinium/day=53.96+46.61ln(x), r^2=0.99, n=82

MC #didinium/day=39.2+37.21ln(x), r^2=1.00, n=110

By comparing the functional form of both the Didinium and Paramecium fission rates (given MC or NMC) it appears that the prey can withstand starvation, in terms of maintaining a viable reproductive rate, somewhat better than Didinium. The reason for this may be related to differences between the feeding behaviors of the animals in that the prey can usually obtain some food at any given instant, even at the lowest CC level, while this is not the case for the predator.

Predator Functional Response

Both the results obtained for the NMC and MC systems show the same trend (Figure 5a, b). As the CC levels (prey nutritional quality) drops from CC1.0 to CC0.5 the 'plateau' of the feeding response drops by about half. With the NMC system, this plateau drops from about 12.2 prey/predator/day to 6.4 prey/predator/day. Similarly, for MC systems, at CC1.0, 11.6 prey/day are consumed while at CC0.5 only 5.2 prey are consumed per day. There is no significant

difference between the final plateaus at NMC1.0 and MC1.0 (U = 73, P>0.25, n1 = 14, n2 = 16). There is a significant difference between NMC0.5 MC1.0 (U = 262.1, P<0.001, n1 = 16, n2 = 20). The MC systems exhibit a ' drawn out' response curve, though the general shape still conforms to a type II functional response. This is attributed to the decreased searching rates of the predators in these systems and will be discussed later. The MC curves are also shifted to the right on the x axis, implying the predators are unable to support themselves on lower densities of prey.

The functional response curves can also be used to give an indication of, among other things, the predatory success rate and the time taken in handling the prey (including consumption, digestion, and resynthesis of the feeding apparatus). When the predators are feeding at their maximum rate, they should consume about 12 prey per day, assuming a 2 hour resting phase. This was confirmed by the position of the plateaus in the observed functional response for both NMC1.0 and MC1.0 systems. The maximium feeding rates determined for these systems were 12.2 and 11.6 prey per day.

The CC0.5 functional responses for both treatments level off at a rate significantly less than the maximium expected. Why might this be? For one thing, the capture success of Didinium must now be considered since the predators are not assured a capture at each prey contact.

From the capture success data, it is possible to predict at what rate the plateau in these responses should occur. For NMC0.5, this maximum rate is predicted to be 9.6 prey per day while for MC0.5 this rate is 8.2 prey per day. These are still considerably higher than the observed rates. There are at least three possible reasons for this deviation;

(1) the resting phase for predators grown upon prey raised under CC0.5 conditions is longer than two hours.

(2) the success rate is lower in these cultures: to produce these results it would need to be about 52 percent in the NMC systems and approximately 46 percent the MC systems.

(3) the predators take a longer time to find prey after coming out of the resting phase; in effect they would be satiated for a period; this however does not seem likely considering the CC1.0 data.

There is also additional information that can be gleaned from these curves: the average searching time of the predator at a given prey density. The functional response curve describes the feeding rate of the predator in relation to various prey densities (or ratios). Assume that the predator's resting phase takes two hours, this is not unrealistic for CC1.0. By multiplying this value by the number of prey taken per day at any given prey density, one can obtain the total time spent by a Didinium in the resting phase. Any time remaining is spent in searching for the

prey. By dividing the searching time by the number of prey consumed, an estimate of the average searching time per predator is obtained. In the following discussion only the CC1.0 systems will be considered.

Based on a consideration of the velocities of the predator and the prey, the rate of contact between the components should be about 30 times greater in NMC systems than in MC systems. This is determined from the following relation (Salt, 1967; Stanely, 1932);

$$C = (v)(y)(3.1416)((o1 + o2)/2)^2)/G$$ where

c = the number of contacts /time

v = the mean predator speed

o1 and o2 = the mean diameters of the prey and predator respectively

G = the volume of the system

If we consider the actual functional response data, we find that the actual searching time in the systems can be given by power series. Specifically;

$$\text{NMC searching time} = 10.7X^{-0.67},\ r^2 = 0.95$$

$$\text{MC searching time} = 42.7X^{-0.8},\ r^2 = 0.99$$

By taking the integral of these regressions one can obtain the total searching time of the predator over the designated prey densities. By comparing these times, we find that the time spent searching for a prey in MC systems is only six times greater than in the NMC systems. Also as the regressions suggest, the difference in searching times

between the two systems decrease as the prey density increases. For instance, at a prey/predator ratio of 1, the predators in the NMC systems take about 28 hours to capture one Paramecium ; for MC predators, a time of 118 hours must elapse. At a ratio of 20:1, the NMC predators take about 0.4 hours while the MC predators use approximately 2.2 hours.

It is important to note here that these differences in searching times, particularily at the low CC levels are vital in influencing the outcome of the interaction. Since Didinium barely last 48 hours without food, at low CC levels and prey densities, the predators are severely affected.

Prey Required for One Didinium Division

This parameter is significantly affected by the presence of MC in the system. The number of prey required by Didinium to divide is significantly greater in MC culture than in NMC cultures at all CC levels (Figure 6, Table 5a, b(stats)).

Within a NMC or MC system, there is no significant difference between CC1.0 and CC0.75. Below these levels, a significant difference develops. As CC drops, the number of prey required for a fission of the predator drastically increases. This has also been shown previously; as many as 8 to 12 Paramecium may be required by Didinium to reproduce, if the prey are sufficiently starved (see Butzel and Bolten, 1968; Calkins, 1915).

Prey Capture Success

There is no significant difference between MC and NMC systems at a given CC level, with respect to this parameter. There is, however, a significant difference, within a treatment, between the CC levels (Table 4a, 4b(stats)). Didinium becomes increasingly inefficient at capturing and holding prey as the nutritive state of the prey decreases (equivalent to decreasing CC). The prey used at each CC level tested were grown at that particular concentration. The success of CC0.375 Didinium against CC1.0 prey was only about 24 percent (n=50).

The number of prey that manage to escape the predator after an attack to die a short time later as a result of the venomous effects of the Didinium toxicysts also increases significantly as the CC level reach their minimum values. At CC1.0, virtually all of the Paramecium that escape the grasp of the predators (about 1 percent) eventually die within a few minutes (n=54). At CC0.375, about 50 percent of the prey escape, and of these only 25 percent actually die (n=88). Some of the survivors in the latter group do exhibit subsequent abnormal structual morphology and disrupted mitosis (see Janovy, 1963). It appears that this decrease in the capture efficiency of Didinium may be related to its diminishing size (Table 14) when fed on increasingly starved prey (also see Mast, 1909). The capture success of Didinium

can be influenced by three factors;

(i) *Didinium* Discrimination of Prey types

Many protozoan species ingest almost any edible food, others however, like *Actinobolina radians* and *Didinium* are much more fastidious (Manwell, 1968). It is not known how protozoans are capable of distingushing between edible and inedible substances. In these experiments *Didinium* could distingush between starved and well-fed paramecia. When given a choice between these two types of prey, well-fed *Didinium* selected the well-fed prey a significantly greater percentage of the time. The well-fed *Didinium* picked healthy prey approximately 84 percent (n=60) of the time ($X^2=13.07$, $P<0.001$); starved *Didinium* chose nutritionally adequate individuals only 57 percent (n=60) of the time ($X^2=0.45$, $P>0.5$). This difference was examined and found to be significant ($X^2=6.72$, n=110, $0.025<P<0.050$). In addition, starved *Didinium* generally consumed the first prey they contacted; this was not necessarily the case with the well-fed predators. Starved *Didinium* discharged their feeding apparatus at the first prey contact 87 percent of the time (n=60). Well-fed predators did so only 65 percent of the time (n=60). The difference between these two values is significant at the 5 percent level ($X^2=7.68$, $0.025<P<0.05$). *Didinium* then is able to discriminate between prey species and nutritional types of the same species. The discrimination exhibited here is related to the predator's

nutritional state.

(ii) The Importance of Predator Size

An important characteristic of any predator's functional response is its ability to overcome the prey's inherent mechanisms for defense. Mast (1909:97) described the reaction of Paramecium to Didinium attacks as follows, " If a didinia chances to swim against a paramecium .... the two adhere to one another, and one soons finds a tangle of fine filaments all about the scene". These fine filaments are of course, the trichocyst fibers discharged by the prey in response to the predator's assault. Mast (1909) observed that if the Paramecium is larger than the attacking Didinium , the prey's trichocysts may hamper and throw off the predator. Prey of a size equal to or smaller than Didinium did not inhibit the predator's attack. These observations were confirmed in the present study. Success of the Didinium at capturing a prey is positively correlated with predator size, a parameter itself related to the physiological state of the animal (see Table 14). By correlating the crude size categories of predator given in Table 14 with the probability of success given in table 4a, the correlation value is found to be about 0.95. This high correlation is no doubt due in part to the high degree of arbitariness in the classification of predator size. It does serve to indicate that a relationship between these two parameters does exist. Additional support for this hypothesis comes from the

following experiments. Small CC1.0 Didinium taken immediately after fission, had a success rate significantly less than large CC1.0 predators. The larger predators were successful 95 percent of the time (n=50) while the smaller Didinium were successful only 70 percent of the time (n=50). This difference is significant at the 2.5 percent level ($X^2=6.35$, $0.025<P<0.05$). The smaller CC1.0 predators were themselves more successful at capturing prey than the similarly sized 'normal' Didinium of CC0.375. This difference is statistically significant ($X^2= 6.25$, $0.01<P<0.025$).

(iii) Nutritional Inadequacy and the Toxicysts

The starvation of the predators also seems to affect the relative toxicity of the feeding apparatus; indicated by the greater chance of a Paramecium surviving after escaping a predator (see results). This, no doubt has an influence on the success rate. It was observed in the CC0.375 systems that prey would quite frequently escape the seemingly firm grasp of the predator. Such an occurrence was rarely observed in the CC1.0 cultures and may be due in part to the greater relative strength of the predator and the increased potency of their proboscis toxin.

Excystment of Didinium

The dependency of encysted Didinium upon the bacterial

concentration in the environment for the induction of excystment is clearly shown in Figure 7 (Table 6a, 6b(stats)) (also see Butzel and Horowitz, 1965). The lower the density and reproductive vigor of the bacterial population, the less likely Didinium will excyst. This may play a distinct role in the optimization of Didinium's predatory activity (see discussion).

Rate of Prey Capture Required for Maintenance

These experiments, though crude, do give an indication of the rate of prey consumption required by Didinium to remain alive (Table 7). To achieve 80 percent survival, Didinium grown upon CC1.0 prey need only be fed at the rate of 1 Paramecium/day. However, when fed upon CC0.5 prey, this rate of consumption rises to 2 prey per day. At CC0.375, the rate of prey consumed must be at least 7 per day. This latter result would seem rather high considering the functional response data. This difference is probably a result of the use of different experimental volumes and absolute prey densities between the two experiments. Since the latter experiments were carried out in a much smaller volume than those of the functional response runs, the correspondingly larger volume increases the searching time of the predator and thus decreasing the rate of prey consumption per unit time.

(C) Population Dynamics

Extinction of Component Species at Low Densities

These experiments were performed to give a quantitative indication of how both the variation in the environment and the general mortality factors intrinsic to the animals themselves influence the outcome of an interaction when the population densities of the component species become low. The probability of extinction declines as the number of individuals in the system increases (Table 8). The environment appears to have little effect on the outcome of the interaction at population densities of over 3 individuals/ml. Didinium cannot survive on prey cultured on CC0.1 or CC0.25 medium, therefore no results were obtained for these systems.

Long-term Runs

NMC Systems

With respect to coexistence of the component populations, the results from these experiments are rather straight forward. Neither coexistence nor any trend toward stable oscillatory behavior was observed at any CC level investigated (Table 9, Figure 8). In all cases, except at CC0.1 for reasons mentioned earlier, Didinium completely overexploitated the prey, driving them to extinction, then followed a similar course themselves. These results are

basically those found by Gause (1934). The time to extinction of the systems, increases significantly as CC levels drop. A logarimthic regression to this data gave an r^2 value of 0.95.

Coexistence was achieved in such NMC systems by Luckinbill (1973) by using a relatively large volume of medium (350 ml) and very low CC levels. Two 100ml, CC1.0 cultures, stored at 10°C persisted in this study for over two months, however no quantitative measurements were taken.

MC Systems

Typical results for the long-term runs with MC are presented in Figures 9a and b, 10a and b, 11a and b, 12a and b, and 13. Both time and phase plane plots are given. In addition Table 9 summarizes the important characteristics of the interaction at all CC levels.

Long term coexistence of the component populations was achieved in the systems CC0.5, CC0.425, and CC0.375. The between run statistics are given in Table 10. There is no significant difference between runs of a given CC level. Didinium populations show less variance in numbers than do the Paramecium populations. This was tested by using the peak density values, both high and low, of the component species and performing an analysis of variance on these values. One case of prolonged interaction was observed in a CC0.6125 system.

Systems of CC1.0, CC0.875, CC0.75, CC0.6125, CC0.25, and CC0.1 do not exhibit long-term persistence of the interaction; however the first four concentrations did cycle to some extent, this behavior being characterized by an increasing amplitude of oscillations. A logarithmic regression to the data yielded a r^2 value of 0.91.

The levels CC0.25 and CC0.1 were incapable of producing prey that could adequately nourish the predators. NMC0.25 prey were capable of supporting a limited predator growth. This furthur strengthens the hypothesis of the importance of energy loss by predators in the MC media. This phenomenon of prey not being nutritionaly adequate to sustain the predators has been observed in other protozoan systems (Janovy, 1963) and may account in part, for the survival of prey populations in nature.

Of the coexisting systems, only CC0.5 showed a set of increasing oscillations up to a stable unchanging trajectory. The systems CC0.425 and CC0.375, after a small initial cycle, exhibited damped oscillations. They eventually, however, maintained a stable cycle. The CC0.425 system was characterized by both a larger mean amplitude of the final stable cycle and a shorter period of time required to obtain these stable oscillations than the CC0.375 systems. This was determined by use of an analysis of variance. The four critical points in the phase plane where the trajectory of the systems become parallel to the x or y

axis were tested. These values between the different CC systems were compared with respect to one another. For example the F value between prey peaks of CC0.5 and CC0.375 was 6.74 ($v1=72$, $v2=92$, $P<0.001$). Between CC0.5 and CC0.425 the F value was 3.22 ($v1=72$, $v2=62$, $0.001<P<0.005$) and for CC0.425 and CC0.375 the value was 2.09 ($v1=62$, $v2=97$, $0.005<p<0.01$). Similiar results were obtained by testing the other three critical values.

The derivation of the actual zero isoclines of the predator and prey populations from the experimental data can be accomplished following the example of Goel and Strebel (1972). The isoclines derived for the various systems are presented in Figure 16 and a brief summary of the important aspects of the predator isoclines is given in Table 11. The limits of the observed points are given in Figure 17. Here 90 percent of the observed points observed during various long-term or perturbation runs are delimited. The description of this data will be left to the discussion.

The data used to construct these isoclines must conform, as mentioned earlier, to three conditions. The actual data obtained from this study meet these requirements with one exception. The trajectory of the initial cycle in most of the systems violates condition two by crossing upon itself. Such crossings do ocassionally occur in later cycles. However, these crossings can be interpreted as a result of slight stochasticity in the environment. This is

within the bounds delimited by the condition. It is possible that the crossing of the trajectories during the initial cycle could be due only to environmental variation. Since the size of the populations during the initial cycle is small, any constant mortality induced by the environment results in proportionately greater numerical changes.

This 'initialization' phenomenon, however, has been noted before by Huffaker et al. (1963) and can also be seen in the results of Luckinbill (1973, 1974) and Utida (1957). It is unlikely that such a common occurrence is due entirely to the external milieu. Indeed, this characteristic of newly initiated systems has been attributed to unusually large amounts of food (with respect to the prey) and other factors that are not significant in later oscillations (Huffaker et al., 1963).

In this study, the initialization period appears to be due in part to the lack of a bacterial 'lawn' covering the exposed surfaces of the culture vessel at the beginning of the run (as time proceeds, the entire vessel becomes covered by a layer of bacteria). If coexisting (or non-coexisting ones if taken early enough) were returned to their initial densities, no initialization behavior in the next cycle was observed. It was also found that if a coexisting system was placed in a sterile culture vessel, the initial cycle in this new dish was abnormal with respect to the cycles that had preceeded it.

During the course of this study, it was noted that the volume of the experimental system had important effects on the outcome of the interaction. If the volume of a coexisting CC0.5 system was decreased by two-thirds, with a similar decrease of the existing population density the system did not coexist. Three replications were carried out; the Paramecium were over exploited in all cases and driven to extinction. A control system, where the volume of the culture remained at 6ml, but whose population was decreased by two-thirds, persisted normally after regaining the stable cycle. Systems that were initiated at 2ml volume also exhibited overexploitation of the prey by Didinium. This is rather important since it implies that the outcome of a dynamic interaction is related to the volume of the system.

Perturbations

(i) Numerical Displacement

To refine the definition of the predator and prey isoclines, systems were displaced to new positions in the phase plane after they had attained stable oscillations. All but a few of these systems returned to the equilibrium configuration. By applying an analysis of variance to the critical points it was found that for both CC0.5 and CC0.375 the "re-attained" cycle was not significantly different from the stable configuration (for CC0.5, P=0.87, v1=53, v2=40, P>0.75; for CC0.375, P= 0.61, v1=56, v2=60, P>0.75) (see

Figure 14a, b). It was noted in both cases that systems perturbed to the inside of the stable configuration achieved the stable cycle within one oscillation while those perturbed to the outside took at least two oscillations to achieve the standard cycle (the F value for the first perturbed cycle for CC0.5 is 2.2, v1=43, v2=36, $P<0.01$; for the CC0.375 systems, F=1.8, v1=50, v2=40, $0.01<P<0.025$).

The results of these perturbations were especially interesting around the equilibrium point. Both the CC0.5 and CC0.375 systems, when returned to their equilibrium points, did not remain there but invariably spiralled out to the equilibrium configuration. The actual equilibrium point for a given system was found by approximating the isocline by a least squares numerical method and solving the resulting equations for their intersection point. A number of systems were started in the region around this point since the predicted point was most likely not the actual one.

(ii) Temperature Shock

A number of CC0.5 and CC0.375 systems were subjected to a sharp temperature change during the course of a run. This was done to determine if the results obtained by the physical displacement of the system described above, were the same as those derived less artifically. The 'shocked' systems show a significantly greater chance of extinction than do the control systems (Table 12a, b, c(stats)). The CC0.5 systems are affected by the shock to a much lesser

extent than the CC0.375 cultures. Though in both CC0.5 and CC0.375 cultures the shock severely displaces the populations away from the equilibrium configuration, the displacement of the CC0.375 systems is of a much greater relative magnitude (Table 12b).

(iii) Predation on and Immigration of Didinium

These manipulations were performed only on CC0.5 systems. When Didinium were removed at a rate of 25 percent from the system, oscillations reminiscent of a CC0.425 or a CC0.375 system were obtained (Table 13). Indeed, these results do appear to be intermediate between these two cultures in some respects. These cycles are different from CC0.425 ($0.025<p<0.050$) and are significantly different from the CC0.375 runs ($0.01<P<0.025$) (Figure 14c).

When Didinium were added to the cultures at a 25 percent rate, extinction of the prey quickly occurred. No true cycling behavior was observed.

(iv) Zone of Stability

The sizes of the zones of stability in the phase planes of CC0.5 and CC0.375 systems were roughly determined. The area of instability is much larger in CC0.5 than in CC0.375 (Figure 15a, b). This is a result of the greater efficiency of the predators in the former systems. This data also compares favorably to that obtained from the numerical

displacement experiments. Systems which were displaced to positions outside the stability boundary did not persist, while those started within this region eventually returned to the stability configuration. These experiments were used to give an indication of the zone around the boundary region, represented by the dashed lines in the figure. Within these zones the outcome of the interaction could be either stable coexistence or species extinction. These zones are a result of environmental stochasticity and qualitative differences in the initial starting populations.

Discussion

Characteristics of *Didinium* as a Predator

When considering protozoan predator-prey systems, one is led to wonder why the interactions between *Didinium* and *Paramecium* (Gause, 1934), *Asplancha* and *Paramecium* (Maly, 1969), *Perispira* and *Euglena* (Dewey and Kidder, 1940), or *Leucophrys* and *Glaucoma* (Brown, 1940) are seemingly self-destructive, and why the interaction between *Woodruffia* and *Paramecium* (Salt, 1967) or *Tetrahymena* and bacteria (Canale *et al.*, 1973) persist for extended periods of time in experimental, spatially non-heterogeneous microcosms? Indeed, considering only the results of this study, why does the *Didinium*- *Paramecium* interaction coexist in some MC cultures and not in others, and how do these compare the NMC systems where persistance of the interaction to even a slight degree was never observed? These questions can be answered by considering the characteristics of the predator and the prey, and the structure on the experimental system.

The outcome of the predator-prey interaction in MC systems depends upon the relative contribution of four basic parameters to the dynamics of the interaction at the different CC levels. These four population parameters are;

(1) intraspecific competition within the prey population

(2) the success of predators at capturing prey

(3) the hunting rate of the predators

(4) the fission rate of the predator at different prey densities

Coexistence of the predator and prey, assuming the predators searching rate is constant, is achieved by strong intraspecific competition within the prey population and low predator efficiency. Non-coexistence is a function of low prey self regulation and high predator efficiency.

(1) Prey Capture

The capture success of Didinium depends upon three factors; its ability to discriminate between prey types; its physical size; and the potency of its toxicysts. The effect on the success rate by the latter two factors is obvious. The first becomes important only in the long-terms runs. It implies that when the predator is well-fed it will not consume as many per unit time as it would when starved. This has an influence on the shape of the predator isocline and will be discussed later.

Consider the case where both a well-fed and a starved Didinium have met with an unsuccussful attempt to capture a prey. Since both predators have 'fired' the feeding apparatus, this structure must now be resynthesized with no energy return for the effort. To a well-fed predator, such a failure is not a serious situation. It has sufficient energy

reserves to support the regrowth of the proboscis and allow continued hunting after the resting phase.

A failure, when viewed from the position of a starved predator, however, is considerably more serious. A starved Didinium can ill-afford to waste energy in rebuilding the expended feeding apparatus if there has been no net gain for this expenditure. If its energies are depleted to such an extent that the proboscis can only be partially reconstructed, or if there is no energy left for searching, the predator will die. In the CC0.375 experiments, many predators were seen, after being repulsed by a prey, to go into a resting phase from which they did not recover. Many were seen to be weakly swimming about.

The consequences, therefore, of failure to a starved predator are considerably different than those to a well-fed predator. It is important to remember when considering the dynamics of the different systems, that failures are a general rule, rather than the exception, in the lower CC cultures. For instance, when confronting a starved predator, Paramecium have about an even chance of surviving; however against healthy predators, they have for all purposes, no chance. For the various CC levels between the extremes of CC1.0 and CC0.375, there is a continuous spectrum of predatory success rates. These must be accounted for when describing the dynamics at each CC level. Even within a CC level, as a result of the periodicity of the prey numbers,

and the subsequent oscillation in the states of predator starvation, the success rate will vary as a function of the prey density. The measured success rate only represents a maximum value for this parameter for any given system.

(2) Searching Rate

Didinium is an active, rapidly foraging predator. Because of this bevavior, a great deal of energy would be required by the animal per unit time. This is demonstrated by its relatively short life span when starved. Unlike Paramecium, which is capable of living at least a week in sterile medium, Didinium can survive only two to three days.

Consider the searching behavior of Didinium. Applying the simple aspects of game theory to the experimental system, one can determine the optimal searching patterns available to a randomly hunting predator moving through a volume or along a plane. Game theory is especially useful for giving an indication of the optimal strategies availiable to two antagonistic species since the tactics used by both must be constructed by analyzing the rules of the game. For biological systems, the rules have defined biotic and abiotic limits within which natural selection acts to choose the strategies. For randomly hunting predators, the optimal searching pattern is predicted to be basically one that involves frequent changes of direction; quick turns with short periods of linear movement. This is

just the pattern of response we find in Didinium, Woodruffia (Salt, 1967), and Dipletus, all randomly searching predators. These protozoans are at a disadvantage in that they have no means of sensing out prey. Their survival therefore depends directly on the searching rates and the way hunting is carried out.

Didinium, in addition to turning frequently, spirals along its line of travel. Though it was not determined quantitatively, this spiral had a radius of about 2 times the diameter of the animal. This pattern allows Didinium to search out a greater volume along its line of travel than would a non spiraling predator (about 7 times greater).

The swimming behavior of Paramecium has probably been most influenced by its resources rather than by protozoan predators. Paramecium swim linearly for long periods of time. This is an optimal pattern when feeding upon bacteria which may be more or less evenly distributed throughout the medium (at least in a given area). Any behavior that involved frequent turns would be a waste of energy. Such a behavior would also be useful when searching out new resource concentrations.

For randomly moving predators, the rate of prey capture is directly related to searching velocity. Methyl Cellulose reduces the velocities of the component species and therefore has the effect of increasing the average time between contacts. Luckinbill (1973) determined the swimming

velocities of Didinium and Paramecium in both NMC and MC systems. The average velocity of the predator and the prey in NMC was 909 and 1923 micrometers per second respectively. In MC systems, these rates were reduced to 29 and 47 micrometers per second respectively. This large decrease in the dispersal rates of the species is not directly proportional to the contact rate (see results).

The greater chance of collisions between the predator and the prey in the NMC systems is probably the most important reason why none of these cultures persisted for any period of time. Though the reproductive rate of the predators is also important, it would not seem to be playing the major role in influencing the dynamics. This can be seen by comparing the rates of predator increase in NMC and MC systems with the corresponding degree of stability in such cultures. Take for an example the extreme cases of NMC0.375 and MC 0.5; though the NMC0.375 system's predator reproductive rate is less than the MC0.50's, the MC system is much more stable. This trend is consistent throughout the data. The success rate too is not as important as might be expected, since the capture success between the treatments is not significantly different. Considering the searching rate however, changes in this parameter have a great influence on the dynamics of the interaction. Even at CC1.0, the MC system exhibits some persistence, the interaction lasting about 260 hours; the NMC systems at the corresponding CC level ran only about 10 hours in the mixed

condition.

In NMC systems, the searching rate determines the outcome of the interaction, and because of the predominance of this parameter over all others, there is always only one outcome. Though other factors are involved and do modify the dynamics to some extent (increasing the time to extinction), they exert little influence on the long-term persistence. In the MC systems, as a result of the great reduction of the searching rate, the success rates and other factors to be mentioned later, become extremely important in determing the outcome of a mixed microcosm at a given CC level. The instability of MC0.5 systems whose volume has been cut by two-thirds supports the hypothesis of the importance of the searching rate on the dynamics of the system. Though Methyl Cellulose inhibits Didinium dispersal, in this smaller volume the predators are capable of searching out all the prey.

The importance of the searching rate cannot be overstated. As described in the results, at a prey/predator ratio of 1, MC1.0 Didinium take about 118 hours to find one prey. This is about 70 hours longer than it takes for a Didinium to starve to death, therefore it is reasonable to expect at least some cyclic behavior in the system. In the NMC systems under similar conditions, the searching time for a Didinium is cut to 28 hours, therefore even at low prey densities the predators are capable of eventually finding

some food. In the NMC systems, in all cases the prey population began to decline and was destroyed before any decrease in the predator population was noticed. Since NMC Didinium can find food even at the lowest prey densities before they starve, the complete extinction of the prey is the only possible outcome of the interaction. With the MC predators, most die of starvation before the prey are eliminated and therefore the potential for cyclic behavior between the populations is enhanced.

(3) Number of Prey Required for Predator Fission

Given a sufficient degree of prey starvation, the predator is incapable of division and maintenance no matter how many prey are eaten (Burbanck and Eisen, 1960; Butzel and Bolten, 1968). Prey of this physiological condition were noted in the MC0.1 and MC0.25 systems and in the NMC0.1 cultures. The inability of Didinium to compensate for the nutritive state of the Paramecium by ingesting greater numbers of prey suggests that starved prey may lose an essential substance, or at least have its concentration drop below a threshold that is required for predator growth. The dipeptidase enzyme mentioned earlier is a likely candidate for this substance. Net energy considerations must also however be taken into account.

The loss of the nutritive value of the prey to the predator as CC decreases, can be seen in Tables 4a and 7. As

the CC levels drop, more prey are required both to provide energy for homeostatic processes and reproductive functions. The increased numbers of prey required are directly reflected in the fission rates. Because of Didinium's resting phase, for each additional prey consumed, 2 hours is added to the time per division. From Table 4a, at MC1.0, one predator fission should occur about every 5 hours. However at CC0.375 one division will only occur every 18.8 hours.

(4) Fission rates

It is unfortunate that the outcome of the interaction of a predator and prey in a mixed system cannot be compared to their fission rates recorded under optimal conditions. The growth rate of the prey in a mixed culture is still density-dependent; the predators, however, no longer exhibit ideal growth but increase according to a modified logistic equation where K becomes a function of prey density at any given instant. Due to the interplay of intraspecific competition and predation on the net prey increase, and the dependence of the predator multiplication on the prey density, these growth rates cannot be represented as any simple function of time. Even within a given CC level, the action of the predator on the prey's growth rate, varies in a manner dependent upon prey density.

(5) Influences of the Prey on the Dynamics of the System

At high CC levels intraspecific effects are of minor importance in reducing the growth of the prey population. The major density regulating factor of the prey population is the predator. As the CC level decreases, intraspecific effects cannot be ignored, and indeed in very low CC systems, it plays the major role.

This changeover in the importance of inter and intra specific interactions in the dynamics of the Paramecium-Didinium system can be shown by comparing the peak densities exhibited by both species in the mixed cultures. First consider the prey peak densities by themselves. The prey increase in a density-dependent manner and there is no reason to assume they do not follow this practice in a mixed culture. In the logistic equation (which will be assumed to be modelling the prey growth), the term (K-N)/K has been called the unutilized opportunity of population growth (Krebs, 1972). This term measures the extent of resource availability and indicates the potential for further growth. Since it is a function of prey density it can be used to give a vague idea of the strength of the intraspecific effects operating in the population. In MC1.0 systems, the maximum value for this term (from the peak density) is 0.20. Likewise for MC0.75, MC0.50, and MC0.375 the respective values are 0.31, 0.59, and 0.62. The prey are exhibiting greater intraspecific effects as the CC levels drop. The reason for this may be as follows.

Consider the predator peak densities in the mixed cultures. The ratio of the predator/prey peak densities decreases continuously as CC declines, from 0.88 at CC1.0 to 0.22 at CC0.375 (see Table 9, Figure 18). This indicates the predators are becoming less numerous in these system with respect to the prey and also in absolute terms. At CC1.0 there are 1.1 prey for every predator; at CC0.375 there are 4.5 prey per predator. If we assume that the more predators there are in a system the greater the deleterious effects on prey population growth, then, as the CC level decreases, the predators must be exerting less of an influence on the prey. A better measure of the decline of predator influence on the prey dynamics can be obtained by comparing the ratio of prey to predator density occurring at the predator peak. These values for CC1.0, CC0.75, CC0.5, and CC0.375 are 0.40, 0.82, 1.25, and 2.91 respectively. In the lower CC systems the predators do not exert much of an effect. The intraspecific interactions within the prey population act to regulate the prey growth. The predators at the lower CC levels cause the oscillatory behavior observed in these systems but they are no longer an important factor in determining the persistence or extinction of the prey. At the higher CC levels, the prey population never achieves a density to make intraspecific effects important on the dynamics.

(6) Oscillations in the Systems

The oscillations exhibited by the component populations

in the MC system can be directly attributed to the changing characteristics of the predator. As the Didinium density is increasing, a stage is reached where the fission rate of Paramecium can no longer support the increasing attrition due to the predator; the Didinium consume the Paramecium faster than they can replenish themselves and the prey population begins to decline. If the predators were instantaneously responsive to the prey decline, they too should begin to decrease. This, however, is not the case. As the prey becomes scarce, the predators are still capable of population growth though their high fission rate begins to decline. Eventually the peak predator density is reached. If the Didinium are healthy, they are capable of driving the prey to very low numbers and extinction. Starved Didinium do not reduce the prey population sufficiently to threaten it with extinction (see Table 16, Figure 18).

MacArthur (1970) has stated that the instability of a system can be accentuated by increasing time lags between the component populations. Usually if a system is controlled by feedback loops as is the present system, time delays in response to changing parameters drive the system in such a manner as to produce oscillations of larger amplitude.

In general, larger amplitude oscillations result if the feedback loop is longer than the natural period of the system (Smith, 1974). For a population experiencing exponential growth, the natural period is given by 1/rm.

Though Didinium does not increase in an exponential manner, 1/rm can be used to give a crude estimate (a minimum value) of the natural period. The actual value of rm in the mixed systems is difficult to obtain. However an estimation of this parameter can be obtained from the functional response data. The main failure with this method is that it automatically assumes that all prey densities occur in the mixed system an equal period of time. For the CC1.0 systems the fission rate is found to be about 2.32 and for CC0.5 about 1.33. The natural period then for these systems respectively is 10.3 and 18.1 hours. The actual delays in the system can be determined from the data concerning the number of prey required per predator division. For the CC1.0 cultures, the delay is about 5 hours while for CC0.5 it is 18.8 hours. These results are not consistent with the above discussion on the stability and size of the oscillations in a system. This time lag of the Didinium population is associated with increasing stability and with the increasing numerical requirements for prey for one fission and since the predatory population is also exhibiting increased maintanence costs, the reasons for this stabilization is obvious and has been discussed earlier. Though the oscillatory behavior of the Paramecium- Didinium system cannot be understood without accounting for the time-delays inherent in the populations, their importance in the direction of the dynamics is greatly influenced by the CC level at which they are operating.

(7) Factors Influencing Coexistence

In protozoan systems it is possible to determine the basic characteristics required by the predator to allow persistence of the interaction in a homogeneous environment. Coexisting cultures of Woodruffia and Paramecium have been obtained by Salt (1967), and Brown (1940) has observed cultures that were tending towards coexistence in a Leucophrys - Glaucoma system. These results can be compared to and incorporated with the observations of the present system. The five main factors which are important in the persistance of these systems are as follows;

(1) the predators are inefficient at capturing prey.

(2) the searching rate of the predator is not overly rapid, or, if the predator is adapted to feeding in one particular subset of the environment, when driven to leave this microhabitat by starvation, it becomes even more inefficient.

(3) the fission rates of the predator and the prey should be approximately equal, or, at least the growth of the predator is highly dependent on the prey density. Time lags between the response of the predator density to changes in prey number should be small to reduce the amplitude of the oscillations.

(4) to maintain themselves and reproduce effectively, the predators should consume fairly large numbers of prey and the predator population should begin to decline at relatively high prey densities.

(5) the prey population must be largely self-limited to such an extent that its density never increases sufficiently to allow the predator to exhibit explosive growth.

There is another characteristic of the predator which could promote the continued existence of the interaction with the prey. When the prey population reaches certain threshold levels, the predator encysts, only to excyst when the prey becomes numerous enough to support predator growth. These threshold levels should be rather high to assure the prey's survival. If the predators excysted at low thresholds, the prey population may have been reduced to such an extent that it is succeptible to extinction due to environmental variation.

(8) The Significance of Excystment and Encystment in Didinium

Encystment of Didinium in long-term systems occurred only at a significant rate in the MC0.6125 (5 percent) cultures and the MMC0.5 (10 percent) and MMC0.375 (20 percent) systems. Encystment was not observed in Gause's

(1934) and Luckinbill's (1973) studies. Though the lack of encystment of Didinium in the experimental systems simplifies the analysis of the interaction, it is not characteristic of the animal. Why encystment fails to occur in these systems may be a result of two pecularities involved in this process. It has been found that Didinium grown under optimal conditions are incapable of encysting when the food supply is rapidly decreased (Butzel and Bolten, 1963). Didinium are also incapable of encysting when either starved or fed on starved prey. The magnitude and rapidity of the numerical oscillations of the prey in the higher CC levels in combination with the resulting starvation of the predator after the prey declines may account for the lack of encystment. At the lower CC levels, the degree of starvation of both the prey and predator may be sufficient to prevent encystment.

Excystment may be due to some metabolite of the bacteria. This characteristic of the predator demonstrates how the nutritional condition of the prey has played an important role in the evolution of Didinium. By excysting only to the presence of sufficient prey resources, the predator is assured of a prey whose nutritional quality is capable of permitting successful predator growth and encystment when the prey again becomes scarce. If the predator excysted only to the presence of the prey, its future would be largely a function of chance. This is because the predator has no means of determining whether the

prey that are availalible are adequate to serve its needs (within the cyst at any rate). It can be safely assumed that, if the prey themselves induced excystment, relatively large numbers of them would be required in the environment. By the time these critical numbers were reached, the prey would most probably be near the point of exhausting their resources (since in natural systems population growth would be some type of pulse function). The predators therefore would only catch the tail end of a once much more vigorous prey population.

By excysting to the prey resource concentration itself, the predator is capable of following the prey's increase, thus prolonging the time that the interaction occurs. This is done by regulating the degree to which the prey exploit the environment. Regulation is achieved through the inhibition of the natural rate of increase of the prey population. Though the prey would not reach the high densities characteristic in the absence of the predator, these relatively lower densities would be maintained for longer periods. In natural systems, large numbers of bacteria would also serve to attract Paramecium and thus assure the predators of at least some prey, sufficient to support a small population, until the prey's growth rate makes up for this initial deficiency. It is unlikely that upon excysting, Didinium would find no prey about. It would therefore be a distinct evolutionary advantage for Didinium to excyst to the bacterial concentration in the habitat.

The experimental data supports the above discussion. The Didinium only excyst at CC levels that support vigorous, healthy prey. At the lower CC levels, where the prey are nutritionally inadequate for the predator, the excystment rate of Didinium is either very low or it does not occur at all. Unfortunately any furthur discussion on this point is limited since in the more natural NMC systems instability at all levels results. Any relationship between excystment, stability and MC level is purely coincidental.

In summary then, the dynamics of the NMC systems are governed directly by the predatory searching rate. The dynamics of the MC systems are however, influenced by the predator capture success, the prey and predator fission rates, and the prey intraspecific effects. The attack success of the predator in combination with the increased numerical requirement of prey for maintenance and division serves to severely limit Didinium's growth potential.

Model for a Protozoan Generalist or Specialist

There is one major factor required by such a model: the predator growth must be directly influenced by the rate of food intake. A simple equation for the predator's numerical increase can be formulated in terms of the searching rate, the capture success, the quality of the food, and the maintenance costs to the predator. Assume the predator has a number of prey species (Pi) from which to choose. Evolution

acts so as to maximize the expected energy gain for the time spent in consuming and digesting any given Pi. To attack and consume a prey, a certain amount of time is taken up, time that could be spent searching for other prey. The total searching time (ST) spent by the predator can be given by $ST=1-\Sigma AiWi$ where Ai is the number of attacks on Pi per unit time, and Wi is the time wasted handling the prey. The total number of attacks on any Pi then is

$$Ai=kPi(1-\Sigma AiWi)Ei$$

where k is a constant of proportionality and Ei is the probability that the predator attacks the prey when it contacts it. The total number of attacks occuring in any given period is

$$Ai=(k\Sigma PiEi)/(1+k\Sigma PiWiEi)$$

The growth rate of the predator must be a function of the prey intake minus the energy expenditures or

$$dy/dt = y(\Sigma AiSiGiQi - M)$$

where

Si is the probability of success against Pi

Gi is the net gain form Pi

Qi is the nutritional adequacy of the prey and

M is the maintenance costs to the predator

This equation can also be given by

$$dy/dt = y((k\Sigma PiSiGiQiEi)/(1+k\Sigma PiWiEi) - m)$$

Natural selection can act on both M, Si, Gi, and Qi to maximize dy/dt for a given resource. But these factors do

not decide the policy that the predator takes, that is, either becoming a generalist or a specialist. The parameter Ei determines this.

If the predator spends most of its time searching for prey, the St is close to 1. In effect, Ai=k PiEi which suggests that selection will maximize the term k PiEiSiGiQi in the growth rate equation. For all prey for which SiQiGi give a positive value, the selection acts to maximize Ei for all prey encountered. If specific resources for the predator are few and far between, the predator should be a generalist.

If ST is small, this indicates that the prey are more numerous or at least easier to find than in the above case. Here, most of the predator's time is spent in handling the prey. Selection now acts to maximize
kPiEiSiGiQi/ΣPiEiWi.

This will be done by optimizing Ei only for those prey species which are the most abundant or yield the greatest net energy gain to the predator per capture. Therefore, if the predator requires considerable periods of time to handle the prey, its best strategy is to consume only those prey that maximize the net energy input per capture. The consumption of the prey requires lengthy periods and the predator cannot afford to waste time consuming less than adequate prey.

Paramecium fall into the category described by the first case. The handling time for their prey, bacteria, is minimal and in addition, their method of capturing the prey also precludes any degree of selective preference.

Didinium can be grouped into the last case. The consumption of prey requires a great deal of time, and the predator cannot afford to eat anything that comes its way. As mentioned earlier, it is obligate on Paramecium, a relatively large prey. Consuming smaller prey would not gain the predator anything in so far as time goes. Consumption of smaller prey might cut down the digestion time, however this process only takes up about 1/4 of the resting phase. The loss in potential energy input for the gain in searching time is not sufficient to change Didinium's selective behavior.

Whether a protozoan predator takes up the generalist or specialist strategy depends upon its method of handling prey, and in addition, the size of the prey itself.

The Isocline Theory

As shown in the first section, the stability of two interacting populations may depend on a combination of many factors. Their degree of influence on the dynamics may vary directly with the biotic and abiotic conditions of the system. Because of the uncertainties involved, prediction of the stability at any given CC level would be difficult unless the correlation of the entire sequence of stabilities with the biological parameters was already pre-determined. A much simplier method of determining the stability of a given system is to apply a graphical analysis. The shape and form of the isoclines and their positions can be qualitatively expressed in terms of the biological characteristics of the component species. Given any system, if the isoclines for the components are known, one can immediately determine the stability of the system in terms of the species parameters.

(1) Isoclines

As described briefly earlier, the isocline method of Rosenzweig and MacArthur was based upon a consideration of the equilibrium points in the predator-prey phase plane; the population densities for which at least one of the species involved neither increases nor decreases. This techinque was developed as a result of the application of differential equations tc natural systems in an attempt to predict their dynamics. The predator-prey phenomenon can be described in

this form since it involves a time derivative.

Predator-prey interactions are observed as changes in the population density of the component species as a function of time. Under special circumstances, these changes are periodic or nearly so. By studying such interactions in the phase plane, time is reduced to an implicit variable and the oscillations of the populations can be coupled together and analyzed as such.

To determine the zero-isocline of the component species in a system, the equations representing the growth rates for each species are solved at the equilibrium points, for example, in a two species system, the equations of the interaction can be given by

$$dx/dt=f(x,y),\ dy/dt=g(x,y)$$

which states that the growth of the population of either species is a function of both species. The isocline of a given species, say x, is found by solving $dx/dt=f(x,y)=0$. This equation determines under which conditions or densities of x and y there will be a steady state for species x. Similiarly solving $dy/dt=0$, we obtain the steady state values for species y. There are two specific types of equilibrium points in the phase plane with which we are the most interested: those where the isoclines of the component species cross the co-ordinate axes and those where the isoclines intersect with each other (Hassel and May, 1972).

To determine the isoclines for an experimental system,

one could merely hold x constant and allow y to reach an unchanging value. This procedure would be performed for all values of x and, as the final result, we would obtain a set of values of x which are associated with at least one value of y which neither increases nor decreases. By varying the values of y for a given x, we would also find that any value of y greater than the steady-state value would decrease, and any value of y less than the steady-state value would increase. By performing the same procedure, but this time holding y constant and allowing x to vary, we would obtain the isocline values for x. The actual execution of this method is extremely tedious and presents considerable techincal difficulties.

The isoclines can be approximated much more simply by the methods of Maly (1969). Here, one observes the initial behavior of a system at any given composition of x and y, realizing that the two orthogonal components of the trajectory at any instant can be represented by a single resultant vector. By using enough points in the phase plane, the direction field of the trajectories can be determined. In the present study, this method was found unsatisfactory due to its dependence upon the sampling time. The presence of a prey isocline was never indicated in the NMC systems, and could only be crudely obtained in the MC systems. The position of the predator isocline was found to be directly dependent upon whether the system was sampled at 6, 8, 12, or 24 hours.

The simplest means to obtain the isoclines of a system can be achieved by observing the behavior of the trajectory over time. This entails merely starting the system at an initial density and counting the populations as time proceeds (Leigh, 1971; Luckinbill, 1973). A steady state is considered reached when the trajectory runs parallel to either of the axes. This was the method used in this study.

The prey isocline can also be constructed from a consideration of the predator functional response (Rx) and the prey growth rate (Gx). This is accomplished by plotting Gx and the family of curves for y(Rx) for various values of y against x. The prey isocline runs through those points where Gx and y(Rx) intersect. This method was also used in this study; however it failed to produce the observed isoclines derived from the data.

(2) The Graphical theory and the Experimental System

(i) The Shape of the Isoclines

The prey isocline derived for all the MC systems are of the predicted convex shape. This is not directly apparent in the MC1.0 and MC0.875 systems because the prey population never achieves a sufficient density to show the region to the right of the hump.

When considering the higher CC levels, the shape of

these isoclines are more or less symmetrical. A distinct asymmetry develops in the lower CC systems (MC0.6125 and less) characterized by a compression of the isocline to the left of the hump and an extension and shallowing of the slope of the isocline to the right of the hump. What is the meaning of this asymmetry?

The cause of the positive slope in the prey isocline to the left of the hump is a result of biological factors. As the number of prey in the system approaches zero, the density of the predators required to stop any futher increase of the prey also approaches zero. Therefore, at low enough prey densities the prey isocline will have a positive slope. The slope of the prey isocline to the right of the hump is negative as a result of the increasing influence of prey intraspecific effects on the dynamics of the prey population as K is approached. As in the above case, fewer predators are required to prevent futher increases in prey density. Rosenzweig (1969) has given a type of mathematical support for the shape of the prey isocline based on a consideration of the intersection of the predator functional response rates and the prey growth rates.

The increasing asymmetry of the prey isoclines at lower CC levels implies then that prey intraspecific growth inhibiting factors are of a much greater relative importance than they are at the higher CC levels. At the higher CC levels, the deleterious action of the predators on the prey

reduce the *Paramecium* density to such an extent that intraspecific density-dependent factors do not exert much influence.

The functional form of the isoclines can be derived from the data by either inspection or by the application of a numerical method of approximation (Goel and Strebel, 1972). If the systems are reasonably well behaved, the isocline method of analysis can be applied to them. By regression of the critical points obtained from the experimental systems, the predator isoclines in all systems, within the limits observed, can be represented by a straight line exhibiting a deviation from the normal towards the right. As the CC level decreases, the extent of the deviation becomes more pronouned and, in addition, the isocline itself exhibits a shifting towards the right along the prey axis (Table 11). What does this rotation and translation of the predator isocline mean in terms of the systems dynamics and its biological significance? To maintain a predator, a discrete number of prey are required per unit time. Below this level of prey consumption, the predator cannot maintain its homeostatic mechanisms and as a result soon dies. This was shown throughout this study. In theory, the slope of the predator isocline is given by the reciprocal of the minimum number of prey needed for maintenance (Strebel and Goel, 1972). It is logical to assume that to survive, each predator requires a certain number of prey, say z. Therefore the mininium number of prey

required to support the predator population is z times the predator density. If the actual number of prey consumed/predator is less than z, the the predator population declines; if the number of prey consumed exceeds z, the predators increase. Therefore the predator isocline must be given by a line with a slope of 1/z, and in the ideal case, with an intercept of zero. The value of z predicted from the slopes of the observed isoclines, is far less than that actually observed by approximately a factor of ten in all cases. This difference can be explained both in terms of the inability of the predator to utilize the prey to the fullest and the time-lags inherent in the process of prey capture and consumption. The theory assumes the complete and instantaneous transformation of prey biomass into predator substance.

The tilting of the predator isocline to the right usually indicates that the fitness of the individual predators is reduced as a result of social disoperation occurring at high predator densities. Didinium does not demonstrate such intraspecific interactions in the usual sense. In these systems, the tilting of the predator isocline can be ascribed to three causes.

(1) The discrimination of the predator at choosing prey.

(2) At high predator densites, the ratio of the prey to the predators is considerably reduced from that at low

densities. The prey population under the influence of such relatively large predator densities, is undergoing rapid change. Only when the predators are relatively rare can the prey achieve a density that results in a prey/predator ratio that favors rapid Didinium increase. When the predators are approaching their peak densities, the prey are rapidly decreasing and have been for some time. As a result, Didinium now find that they must expend relatively more energy per prey capture at high predator densities than at low ones since the prey are now becoming quite sparse and difficult to find. Because of this effect, more prey will be required to support the predators during the upswing of their cyclic oscillations on the basis of the longer predator searching time.

(3) It is also possible that at higher densities of Didinium, the chances of two or more predators capturing the same prey is greater relative to low predator densities. This would reduce the amount of prey 'functional biomass' consumed per capture. It was observed in the systems of this study that this type of 'sharing' of the resource was much more common in the cultures at high predator densities than at low ones (about 15 percent at high densities and for all purposes 0 percent at low densities). After capturing a prey, Didinium becomes more or less stationary for a minute or two, completing the ingestion of the Paramecium. This, at high predator densities, is ample time for another predator to 'capture' the prey once more. This effect, though it may

be even slightly more exaggerated in the high CC systems as a result of the higher mean predator density, might not be so noticeable on the dynamics of the interaction. One-half, or even less, of a well-fed prey is considerably more nourishing than a whole starved one.

The shifting of the predator isocline to the right on the prey axis reflects both the decreasing efficiency of the predator, and the decreasing nutritional quality of the prey. Since more prey are required for the mere survival of the predator at the lower CC levels, the predator isocline must shift to the right.

(ii) Evolution of the Predator Isocline

Evolution has acted on Didinium so as to push its isocline as far to left as is possible. Didinium have not evolved mechanisms for self-stabilization which overcome the destabilizing effects caused by the selective forces in pushing the predator isocline to the left. They have instead, engineered a means by which they can destroy the prey with relative immunity to the effects of the resulting collapse of the system. They are, as discussed earlier, capable of encysting. It is possible that the evolution of a self-stabilization mechanism in a predatory species requires more elaborate and intricate responses than Didinium or any other protozoan predator could possess. In the NMC systems, the resulting interactions were so unstable that no true

cycles developed. In one of the NMC1.0 cultures, the prey population barely increased by one-half before being destroyed (Figure 8).

(iii) Nature of the Oscillations

In the MC systems varying degrees of stability in the mixed microcosms were obtained. When the equilibrium point is to the right of the hump, the oscillations of the system damp down to a stable configuration. When the intersection of the isoclines is to the left of the hump, the systems exhibit increasing amplitude of oscillations and intersect the axes. When the static point is about the hump, stable, constant amplitudal cycles result. The perturbation runs support this contention (Figure 14a, b). If a system was perturbed either to the inside or the outside of the stable configuration, as long as it was within the bounds of the region of stability, the orginal cyclic behavior was eventually assumed.

The oscillations observed in the populations with time could be either inherent in the system itself or due to the abiotic environment. With respect to the latter possibility it is now pertinent to include the following results.

The possiblity existed that the stable oscillations of the coexisting systems were a result of an outside forcing function which was due to some factor in the environment or the experimental design itself. This possibility was tested

in the following manner. The periodic behavior in the cultures may have been as a result of at least two major outside influences.

The observed behavior could have been due to the periodic input of prey resource into the culture. To test this, every 12 hours fresh bacteria were introduced into the system in excess of that required by the prey. The system was still renewed every two days. Four systems were run in this manner and it was found that the behavior of these cultures were for all purposes identical to those of the control microcosms ($F=1.82$, $v1=18$, $v2=62$, $P>0.25$).

The second possible forcing function could have been due to the effects of the the renewal procedure itself in removing metabolite buildup. The test here was to let the system run five days before renewal of the media. Fresh bacteria were still supplied every two days. Again four systems were run and again, the behavior was characteristic of the controls though the prey peak densities were somewhat lower than before (about 8 percent, $0.025<P<0.050$). From these results it can be concluded that the cycles exhibited by the interacting populations were due to the inherent properties of the system and not a result of the experimental method.

(iv) Manipulations of the Predator Isocline

A means of partially separating the effects that the

shifting and tilting of the predator isocline brings upon the dynamics of the system can be seen in the manipulation of the predator density experiments. Shifting the predator isocline to the right by applying 25 percent predation upon the Didinium population noticeably stabilizes the interaction (see Figure 16), while the immigration of predators into the culture quickly collapses the system, even more rapidly than might be expected. Cyclic behavior was never observed and these runs were much more reminiscent of NMC cultures.

The 25 percent predation experiments appear similar to the CC0.425 runs. Using analysis of variance there is no significant difference between the numerical amplitude of the oscillations of these two systems ($0.1<P<0.25$) or between the cycle time ($0.5<P<0.90$). This brings out an interesting point. By imposing 25 percent predation on a CC0.5 system, the interaction has been effectively changed to one of another CC level. It might be expected that in the CC0.425 systems the net predator increase should be about 25 percent less that in CC0.50. The fission rates in CC0.425 systems were never determined directly. They can however, be extrapolated from the data. The extrapolated value is 2.88 divisions/day, about 25 percent less than the CC0.50 value (3.82). This indicates the importance of the division rates in MC systems in influencing the dynamics of the system. This however is not quite as it looks, since 3.82 is the optimal rate which is rarely exhibited in the mixed

cultures.

Two additional runs mentioned briefly earlier were also performed. Predation was applied to the Didinium in the following manner; 0 percent when the predator density was less than 20/ml, 12.5 percent when the population was between 21 and 40 individuals/ml, and 25 percent when the density was greater than 40/ml. Despite the large variation in the points (see Figure 17), there is a tilting of the predator isocline to the right, with almost no compensating shift to the right. The dynamics of this system appeared similar to the 25 percent straight predation experiments and the MC0.425 cultures. This suggests that the angle at which the predator isocline intersects the prey isocline plays little importance in the outcome of the dynamics (at least as long as the orgin of the predator isocline is to the right of the hump). The position of the equilibrium exerts the main controlling influence on the dynamics of the system.

(3) Equilibrium Points in the Stable Systems

Rosenzweig and MacArthur's model predicts quite well the dynamics of the present system, if, we include the restriction that the equilibrium point can be represented by a stable configuration (see May, 1974). Basically we are integrating into the graphical model (though it is already there implicitly), Kolomogorov's theorem on stability of

singular points in the phase plane and the inherent time-lages in the predator population.

The major difference between linear and nonlinear oscillations is that with the latter the amplitude of oscillation of a negatively damped, statically stable, nonlinear oscillator, commonly tends to a finite limit. The limiting periodic oscillations of finite amplitude exhibited in the stable MC systems indicate that, as was also implied by the curve fits to the prey isoclines, higher order terms in the interaction between the component populations are involved. These terms are not biologically apparent in the system.

The equilibrium points observed in the experimental systems were never found to possess any sort of neighbourhood stability. All systems started at these supposed points spiralled out to the stable cycle configuration. There are two explanations for this behavior. The first is that there are no stable equilibrium points for the systems and all 'solutions' are periodic. This is in accordance with the concepts mentioned in the above paragraph. The second explanation is that there is an equilibrim point for the system but its domain of attraction is rather small. The amount of environmental variation acting on the system, however slight, is sufficient to displace the trajectory away from the equilibrium to such an extent that it finds itself in the zone of attraction of the

limit cycle. This interpretation is not biologically unrealistic for zones of attraction around supposed limit cycles in natural populations have been implied to exist (see Holling, 1973).

The equilibrium point in the Paramecium- Didinium system may possess neighbourhood stability with the corresponding zone of attraction (under the given conditions) being very small, so small in fact that it may be considered biologically unrealistic in this case. If every environmental factor was held absolutely constant, a stable equilibrium point might be found. Though the graphical model would now fit the system with no modifications, its purpose is defeated. If it is to be of any practical value it must relate to natural, stochastic systems. Canale's et al. (1973) system held under rigidily controlled conditions does exhibit all the properties predicted by the graphical model. It is however unlikely that the system would behave as such in the 'wild'.

The behavior of the Didinium- Paramecium systems must be interpreted in terms of limit cycles whose magnitude of oscillation is dependent upon the relative position of the predator and prey isoclines. As the predator isocline drifts to the left, the oscillations of the population components increase in amplitude; eventually, the magnitude of these cycles becomes so great that extinction of one of the component species occurs. As May (1972:900) states, " Such a

stable limit cycle provides a satisfying explanation for those animal communities in which populations are observed to oscillate in a rather reproducible manner".

(4) Enrichment

Since most of the obvious manipulations of the predator and prey isoclines were achieved by merely varying the Cerophyl concentration in the system, the results obtained here have a direct bearing on the phenomenon of enrichment in biological systems. As can be seen from the present Didinium - Paramecium system, enrichment increases K for the prey. Assume for the moment that the nutritional state of the prey has no effect on the predators. Enrichment of the system then shifts the prey hump to the right. Since the predator isocline does not move, a resulting shift of the equilibrium to the left occurs. With respect to the hump, the predator isocline can be considered to have moved to the left. The effects on a system's dynamics as the predator isocline moves to the left has been discussed previously. If the system before enrichment is stable, moderate addition of prey resource does not neccessarily shift the equilibrium point to the left of the hump. The system would remain stable and in addition, one would observe an increase in the predators numbers in the system without a corresponding rise in the prey density. This situation was not observed in this study. Though the mean predator population density and its equilibrium co-ordinate does increase with enrichment of the

system, so does the prey's up to a point, after which it declines. The reason for this is a result of the dependence of the predators on the level of enrichment in the system. The predator isocline is not stationary but shifts as a direct function of the prey's physiological condition (itself dependent upon the CC level). It is a result of the movement of both species isoclines that the observed results are obtained. The shifting of the prey isocline to the right and the movement of the predator isocline to the left enhances the instability in the system since the relative movement of the equilibrium point towards and passed the hump is accentuated.

We can draw four general conclusions about the dynamic behavior of this system (and possibly predator-prey systems as a whole) from the experiments presented here;

(1) under certain conditions, when the predator is limited by the prey, periodic fluctuations in the population density may occur.

(2) if the prey is not limited by the predator but rather by its resource, the oscillations of the system tend to damp out though not completely.

(3) a unique combination of inter- and intraspecific effects on the prey will allow a system that exhibits constant numerical fluctuations without damping.

(4) if the predator is limited by some factor other than the prey, damped oscillations may occur under certain situations.

The above conclusions are valid only for a system in which the prey isocline has a hump. Such a maximum, as mentioned earlier, will result only if some of the predator functional response curves intersect the prey growth curve at least twice. Such multiple intersections will occur in a system if; the prey species reproductive rates decline at low densities as well as at high ones, thus indicating an inability of the prey to find mates or such: or, if the reproductive rate of the prey decreases continuously, the predators functional response is a Holling type II curve.

The shapes and positions of the isoclines can be directly related to the characteristics of the component species. The shifting of the predator isocline to the right as the CC level drops is a direct function of the predator's efficiency in the utilization of the prey. This efficiency is affected by the prey's nutritional state. Because of this, the position and movement is directly dependent upon the prey. This explains the simultaneous shifts of the prey isocline to the left and the predator isocline to the right as the Cerophyl concentration decreases.

By incorporating predator time-lags into the graphical model, the behavior of the experimental system can be predicted. Freedman (1976) has shown that there is a region

of the phase plane to the right of the hump where there is an unstable equilibrium but which is bounded by a stable limit cycle. This is the situation observed in the experimental systems. To the right of the hump no stable equilibrium points are observed, however stable limit cycles do occur. To the left of the hump, there are no stable equilibrium points or limit cycles.

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Table 1.

The Accuracy of the Sampling Method as a Function of Protozoan Density

Paramecium		Didinium	
#/ml	% error	#/ml	% error
500	2.0	250	1.2
400	1.6	100	1.5
300	3.3	50	1.5
200	2.9	50	1.9
100	3.6	25	2.5
50	3.8	10	3.1
25	4.4		
10	5.3		

Table 2a.

Paramecium Population Growth Parameters.

Methyl Cellulose Systems

CC	K	rm	runs
1.00	1061	3.14	10
0.875	966	-	10
0.75	838	2.93	10
0.6125	674	-	10
0.50	498	2.66	10
0.425	438	-	8
0.375	381	1.55	10
0.25	191	-	11
0.10	62	0.14	9

Non-Methyl Cellulose Systems

CC	K	runs
1.00	1310	10
0.75	974	9
0.5	562	12
0.375	421	14
0.1	94	10

Table 2b.

Paramecium Carrying Capacity - Between MC and NMC.

	U	P
(i) MC1.0 to NMC1.0	232	<0.001
(ii) MC0.75 to NMC0.75	225	<0.025
(iii) MC0.50 to NMC0.50	279	<0.001
(iv) MC0.375 to NMC0.375	251	<0.001

Table2c.

Growth Rates Determined from the Logistic Equation - between MC Systems.

	U	P
(i) MC1.0 to MC0.75	256	<0.001
(ii) 0.75 to 0.50	220	<0.005
(ii) 0.50 to 0.375	232	<0.005
(iv) 0.375 to 0.10	377	<0.001

Table 3a.

Optimal Fission Rates (per day).

Paramecium

CC	NMC systems fissions	MC systems fissions	runs
1.00	5.15	4.94	45
0.75	4.39	3.79	50
0.50	3.19	2.68	50
0.375	2.54	1.68	40
0.10	1.07	0.49	25

Didinium

CC	NMC systems fissions	MC systems fissions	runs
1.00	5.75	5.27	50
0.75	5.34	4.85	52
0.50	4.43	3.82	48
0.375	3.05	1.07	50

Table 3b.

Optimal Fission Rates - Paramecium

	U	P
(i) NMC1.0 to MC1.0	481	<0.001
(ii) NMC0.75 to MC0.75	521	<0.001
(ii) NMC0.50 to MC0.50	398	< 0.001
(iv) NMC0.375 to MC0.375	362	<0.001
(v) NMC0.10 to MC0.10	429	<0.001
within NMC systems		
(i) 1.0 to 0.75	632	<0.001
(ii) 0.75 to 0.50	432	<0.001
(iii) 0.50 to 0.375	481	<0.001
(iv) 0.375 to 0.10	294	<0.01
within MC systems		
(i) 1.0 to 0.75	721	<0.001
(ii) 0.75 to 0.50	493	<0.001
(iii) 0.50 to 0.375	398	<0.001
(iv) 0.375 to 0.10	288	<0.01

Table 3c.

Optimal Fission Rates - Didinium

	U	P
between treatments		
(i) NMC1.0 to MC1.0	369	<0.001
(ii) NMC0.75	405	<0.001
(iii) NMC0.50 to MC0.50	421	<0.001
(iv) NMC0.375 to MC0.375	622	<0.001
within NMC systems		
(i) 1.0 to 0.75	306	<0.001
(ii) 0.75 to 0.50	629	<0.001
(iii) 0.50 to 0.375	604	<0.001
within MC systems		
(i) 1.0 to 0.75	290	<0.001
(ii) 0.75 to 0.50	376	<0.001
(iii) 0.50 to 0.375	502	<0.001

Table 4a.

Success of *Didinium* at Capturing Prey.

Non-Methyl Cellulose

CC	# successes	# failures	% success
1.00	78	2	98
0.75	76	4	95
0.50	63	17	79
0.375	43	37	54

Methyl Cellulose

CC	# successes	# failures	% success
1.00	96	4	96
0.75	98	2	98
0.50	73	27	73
0.375	48	52	48

Table 4b.

Success of *Didinium* at Capturing Prey - tested by X^2.

	X^2	P
NMC systems		
(i) 1.0 to 0.75	2.96	>0.25
(ii) 1.0 to 0.50	14.2	<0.001
(iii) 1.0 tp 0.375	32.53	<0.001
MC systems		
(i) 1.0 to 0.75	3.21	>0.15
(ii) 1.0 to 0.5	17.2	<0.005
(iii) 1.0 to 0.375	47.1	<0.001
between treatments		
(i) MC1.0 to NMC1.0	0.22	>0.5
(ii) MC0.75 to NMC0.75	0.96	>0.25
(iii) MC0.50 to NMC0.50	0.85	>0.25
(iv) MC0.375 to NMC0.375	0.78	>0.05

Table 5a.

The Number of Prey Required for Fission of *Didinium*.

number of runs for each test is 60

	MC		NMC	
CC	prey	consumed	prey	consumed
1.00		2.4		1.8
0.75		3.9		2.2
0.50		5.8		3.7
0.375		9.4		6.6

Table 5b.

Number of Prey Required for one *Didinium* Fission.

	U	P
between treatments		
(i) MC1.0 to NMC1.0	282	<0.05
(ii) MC0.75 to NMC0.75	395	<0.001
(iii) MC0.50 to NMC0.50	312	<0.001
(iv) MC0.375 to NMC0.375	511	<0.001
within NMC		
(i) 1.0 to 0.75	229	>0.25
(ii) 0.75 to 0.50	310	<0.005
(ii) 0.50 to 0.375	492	<0.001
within MC		
(i) 1.0 to 0.75	254	>0.05
(ii) 0.75 to 0.50	325	<0.001
(iii) 0.50 to 0.375	591	<0.001

Table 6a.

Excystment of Didinium at Different CC's

CC	# excysting	# dorsinant	% excysting
1.00	74	6	93
0.875	75	5	94
0.75	68	12	85
0.6125	44	36	55
0.50	27	53	34
0.425	8	72	10
0.375	2	78	3
0.1	0	80	0

Table 6b.

Excystment in *Didinium* - X^2 statistic.

	X^2	P
(i) 1.0 t0 0.875	0.10	>0.90
(ii) 1.0 to 0.75	4.82	>0.02
(iii) 1.0 to 0.50	31.51	<0.001
(iv) 1.0 to 0.375	80	<0.001

Table 7.

Maintanence Requirements of *Didinium*
20 runs at each density

CC	# prey/day	% survival
1.00	1	83
	2	95
	3	96
0.50	1	45
	2	76
	3	93
	4	95
	5	91
0.375	4	0
	5	14
	6	48
	7	78
	8	82
	9	85

Table 8.

Probability of Component Survival (%) at Low Densities.

50 runs at each density

Paramecium

	initial number/ml		
cc	1	3	5
1.00	95	100	100
0.75	100	100	100
0.5	85	95	100
0.375	55	90	100
0.10	40	80	100

Didinium

	initial number/ml		
cc	1	3	5
1.00	100	100	100
0.75	95	100	100
0.50	70	80	100
0.375	45	60	85
0.10	0	0	0

Table 9.

Summary of the Long-term MC Systems.

CC	runs	K	% 1.0 K	prey peak	pred. peak
1.00	17	1061	-	213	187
0.875	9	966	91	231	177
0.75	18	838	79	258	159
0.6125	4	674	64	271	142
0.50	20	498	47	295	110
0.425	6	438	41	265	82
0.375	18	381	36	235	52
0.25	10	191	18	-	-
0.10	10	62	6	-	-

CC	prey peak % of K	ratio pred./prey peak	coexistance
1.00	20.0	0.88	no
0.875	24.0	0.77	no
0.75	31.0	0.62	no
0.6125	40.0	0.52	no
0.50	59.0	0.38	yes
0.425	61.0	0.31	yes
0.375	61.0	0.22	yes
0.25	-	-	no
0.10	-	-	no

Table 9. continued

Summary of the Long-term MC Systems.

CC	cycles obtained runs	# cycles	condition of predators
1.00	5	2	good
	11	3	"
	1	4	"
0.875	2	2	good
	6	3	"
	2	4	"
0.75	1	2	good
	8	3	"
	4	4	"
	2	5	"
0.6125	1	3	good-fair
	2	5	"
	1	9	"

For the systems of CC0.50 to CC0.375, continuous states of coexistance were achieved. The predators were in a fair condition.

For the system of CC0.25 and CC0.1, the predators were in a poor state and quickly died out.

Table 9. continued

Summary of the Long-term MC Systems.

CC	oscillation type	time/cycle(hrs)	first extinction
1.00	undamped	96	paramecium
0.875	undamped	117.6	paramecium 6 didinium 3
0.75	undamped	134.4	didinium
0.6125	undamped	140.0	didinium
0.50	limit	162	N/A
0.425	damped to limit	145	N/A
0.375	damped to limit	156	N/A

Summary of the Long-term NMC Systems.

CC	runs	K	time to extinction(hrs)	first extinction
1.00	15	1310	10.8	paramecium
0.75	18	974	19.2	"
0.50	14	562	30	"
0.375	18	421	49.2	"
0.1	7	94	-	didinium

Table 10. Between Run Variance in Coexisting Systems.

Analysis of Variance.

0.50 systems	
paramecium peaks	F=1.38
didinium peaks	F=0.93
0.425 systems	
paramecium peaks	F=1.12
didinium peaks	F=0.76
0.375 systems	
paramecium peaks	F=1.83
didinium peaks	F=0.62

Table 11.

Predator Isoclines: Summary of Results.

CC	deviation	x orgin	% prey K	r^2
1.00	3.9°	42	4	0.92
0.875	4.2°	48	5	0.96
0.75	6.4°	78	9	0.95
0.50	9.1°	127	26	0.98
0.375	27.5°	131	34	0.96

Table 12a.

Temperature Perturbation Results.

system type (MC)	initial #	# persisting	% persisting
control (0.5)	15	15	100
control (0.375)	15	13	87
shock (0.5)	15	11	73
shock (0.375)	15	2	13

Table 12b.

Changes in Component Density after the Temperature Perturbation.

system	MC0.5	MC0.375
initial prey #	254	198
initial pred. #	44	26
final prey #	83	22
final pred. #	19	3
% change prey	67	89
%change pred.	56	88

Table 12c.

Temperature Perturbations. X^2 statistic.

	X^2	P
(i) control0.5/control0.375	2.14	>0.15
(ii) control0.5/test0.5	4.62	>0.025
(iii) control0.375/test0.375	16.13	<0.001
(iv) test0.5/test0.375	11.0	<0.001

Table 13.

Numerical Manipulations of the Predator Isoclines.
for control see Table 9

experiment	25% immigration	25% predation	varying
runs	10	11	2
# coexisting	0	10	2
cycle type	undamped	limit	limit
time/cycle	8.7*	12.6	13.2
prey peak	192	256	213
pred. peak	148	71	39

Table 14.

Size of *Paramecium* and *Didinium* at various CC levels (in microns).

the prey are represented by an ellipsoid of semi-axes a, b, and c.

the predators are fit by a Frustrum of a right circular cone of radii d and e and of heigth h.

Paramecium

	a	b	c	volume (microns^3)
MC1.0	20	80	30	2.01×10^5
MC0.5	14	60	22	7.7×10^4
MC0.375	10	50	18	3.8×10^4

Didinium

	d	e	h	volume (micron^3)
MC1.0	40	60	75	1.2×10^6
MC0.5	25	35	60	3.4×10^5
MC0.375	15	20	45	8.7×10^4

% change	*Paramecium*	*Didinium*
1.0 to 0.5	61.5	71.3
1.0 to 0.375	81.3	92.7
0.5 to 0.375	53.3	74.5

Table 15.

Prey Low Mean Density.

CC	prey low density
1.00	8
0.875	11
0.75	21
0.6125	32
0.50	46
0.425	92
0.375	128

Figure 1.

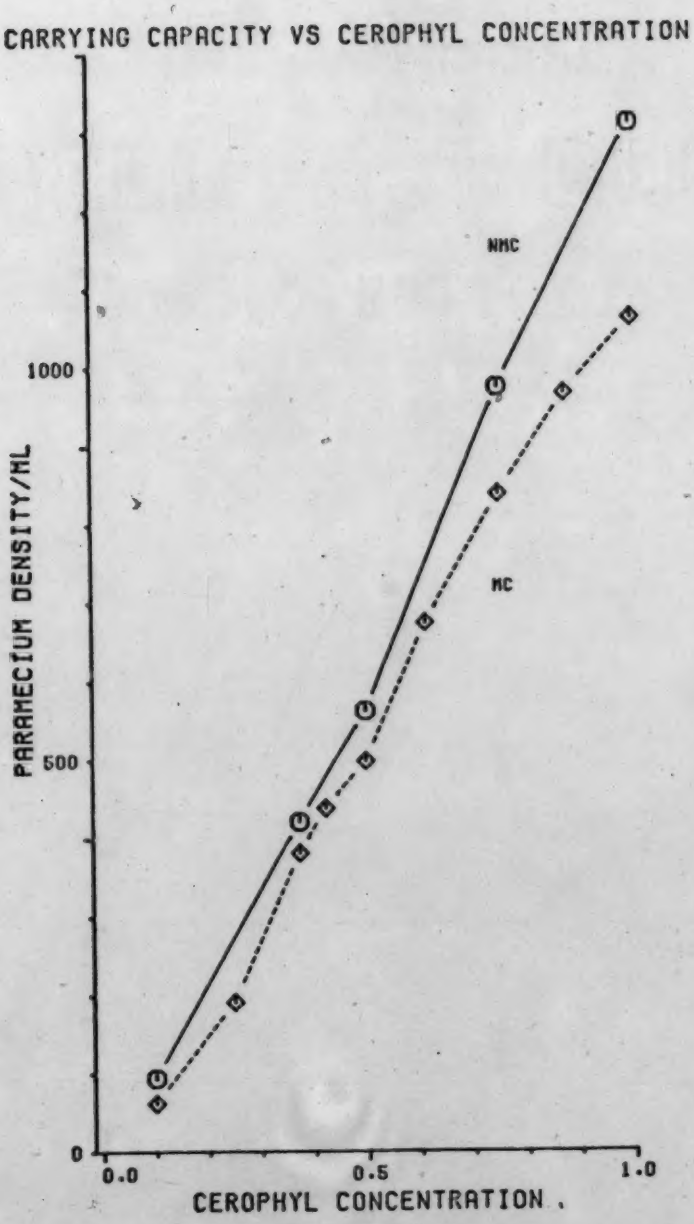

CARRYING CAPACITY VS CEROPHYL CONCENTRATION
PARAMECIUM DENSITY/ML
1000
500
0
NMC
MC
0.0
0.5
1.0
CEROPHYL CONCENTRATION .

Figure 2a.

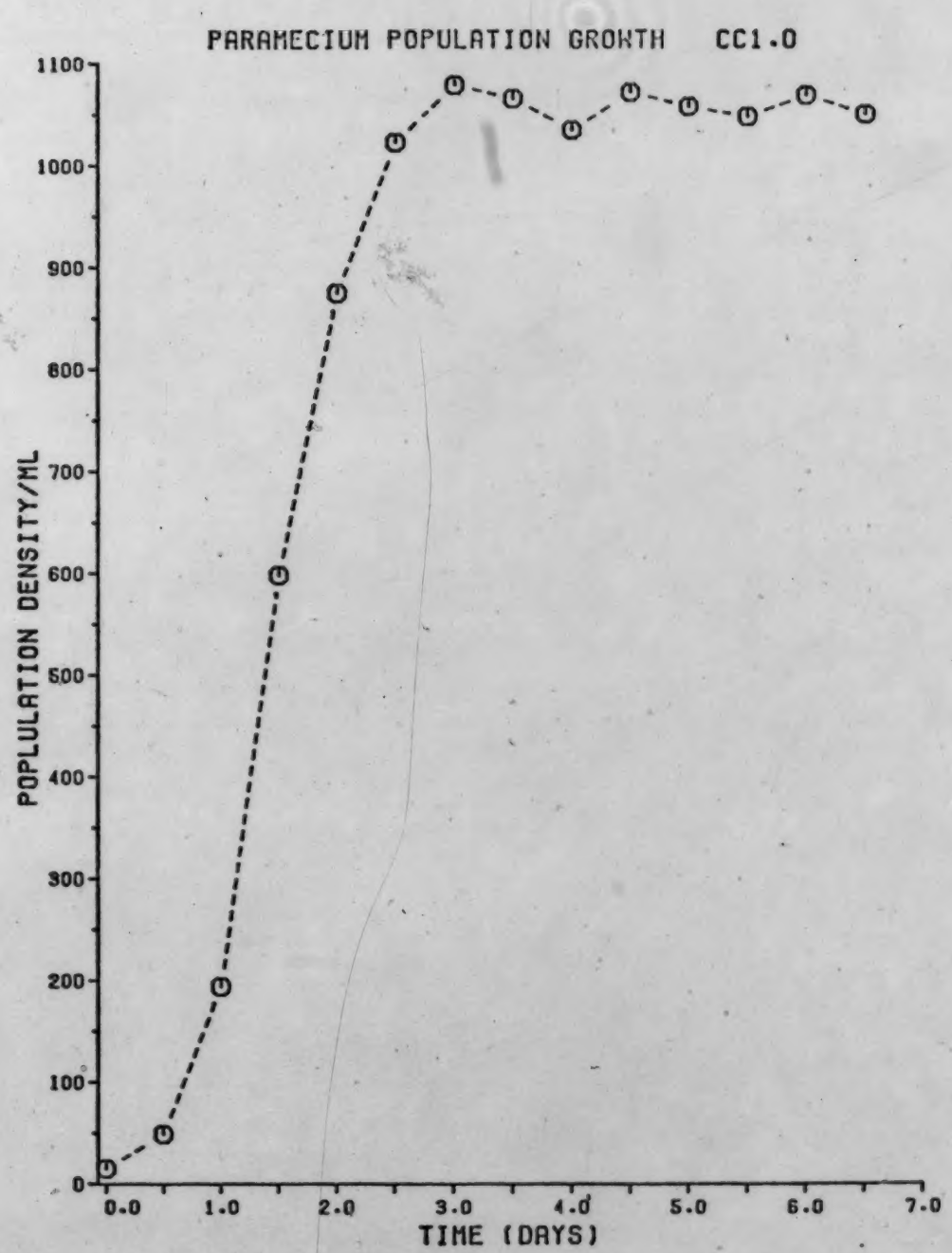

PARAMECIUM POPULATION GROWTH CC1.0
POPULATION DENSITY/ML
1100
1000
900
800
700
600
500
400
300
200
100
0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
TIME (DAYS)

Figure 2b.

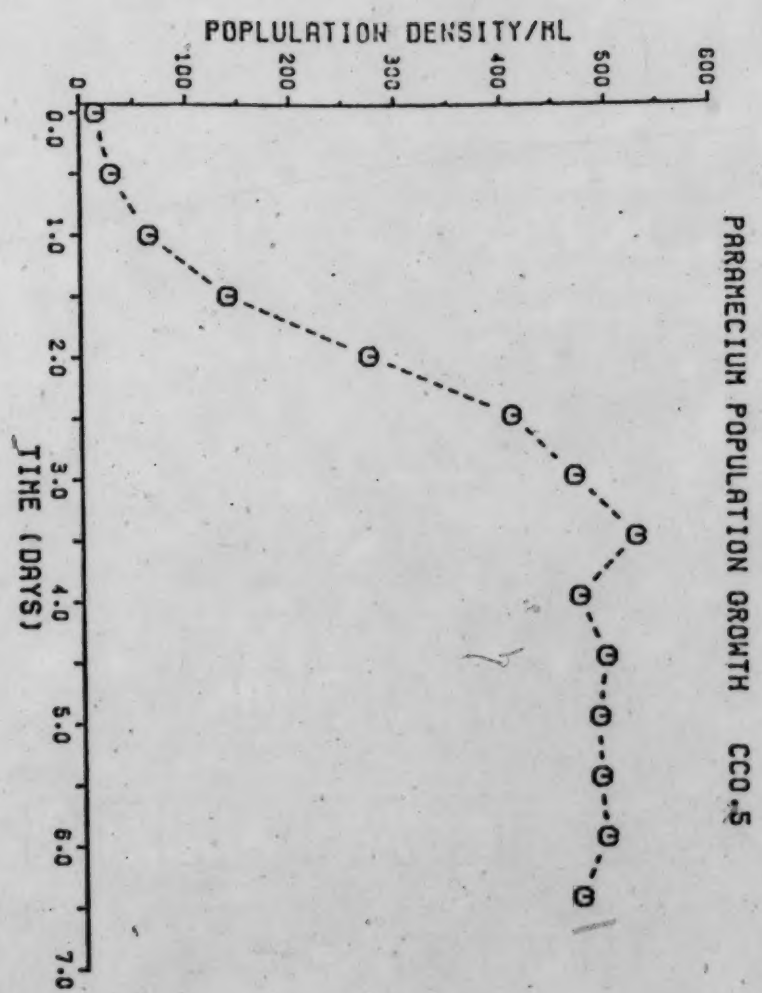

POPLULATION DENSITY/ML
0
100
200
300
400
500
600
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
TIME (DAYS)
PARAMECIUM POPULATION GROWTH CCO.5

Figure 2c.

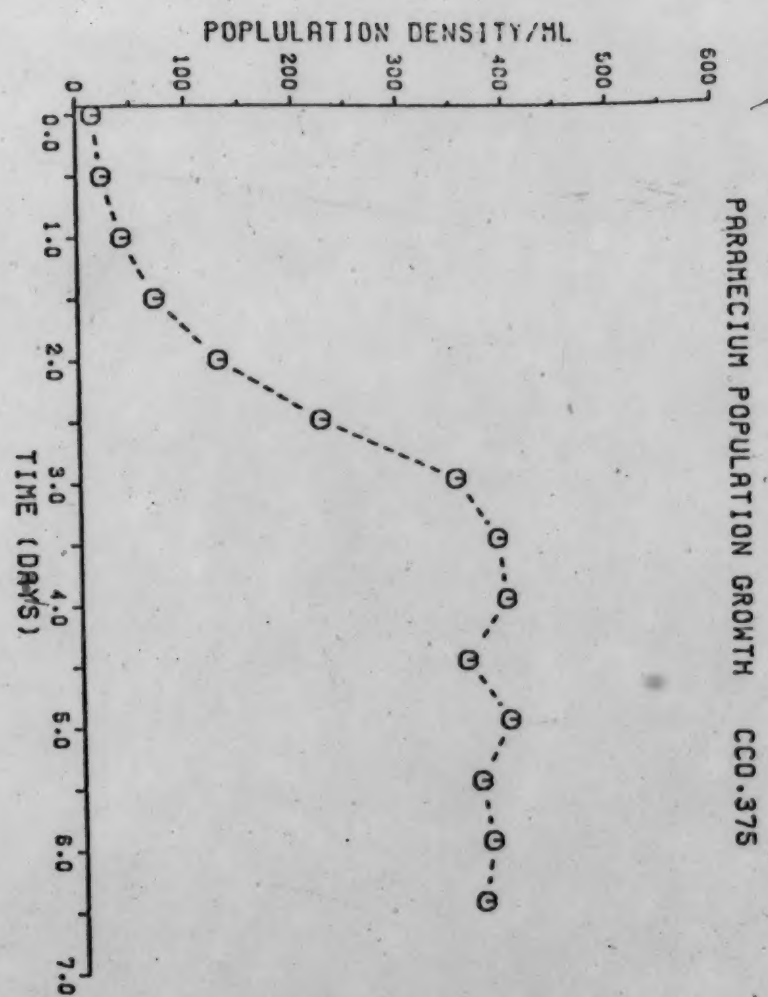

POPLULATION DENSITY/ML
0
100
200
300
400
500
600
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
TIME (DAYS)
PARAMECIUM POPULATION GROWTH CCO.375

Figure 2d.

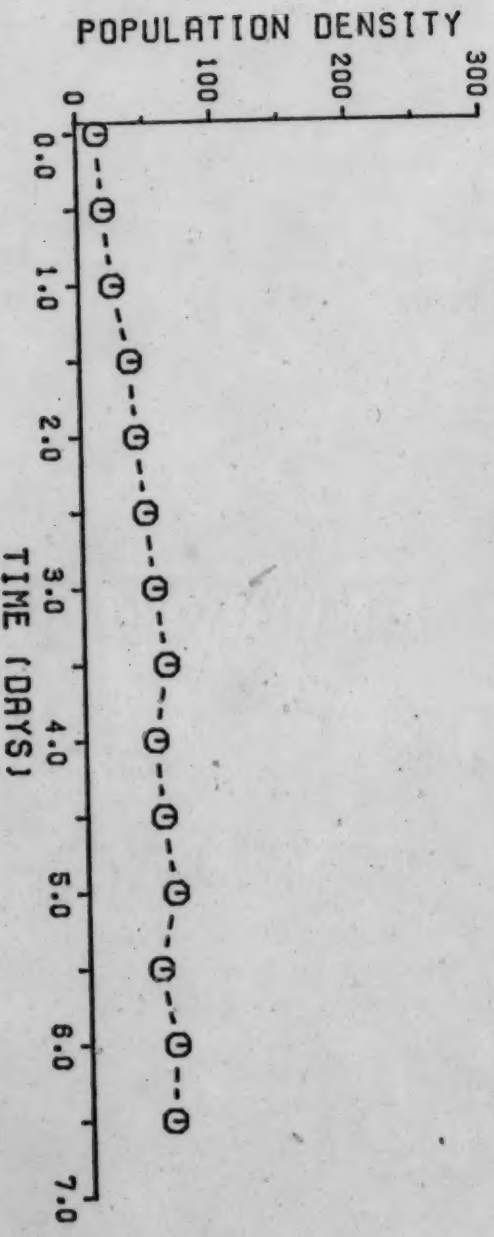

POPULATION DENSITY
0
100
200
300
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
TIME (DAYS)
PARAMECIUM POPULATION GROWTH CCO.1

Figure 3.

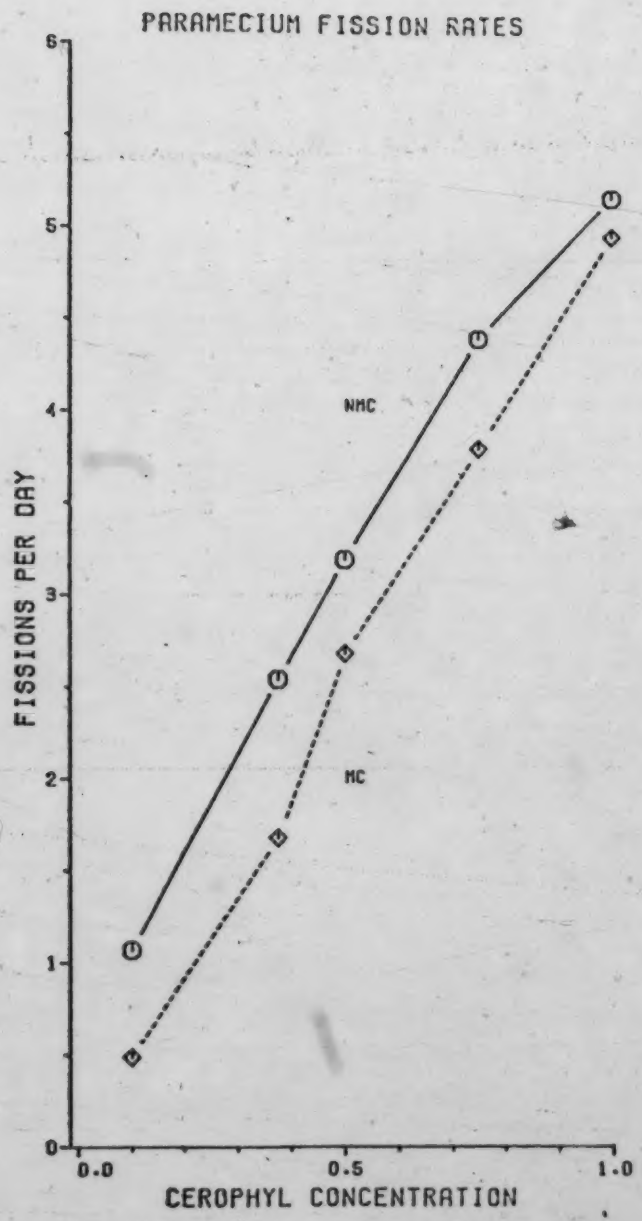

PARAMECIUM FISSION RATES
FISSIONS PER DAY
0
1
2
3
4
5
6
NMC
MC
0.0
0.5
1.0
CEROPHYL CONCENTRATION

Figure 4.

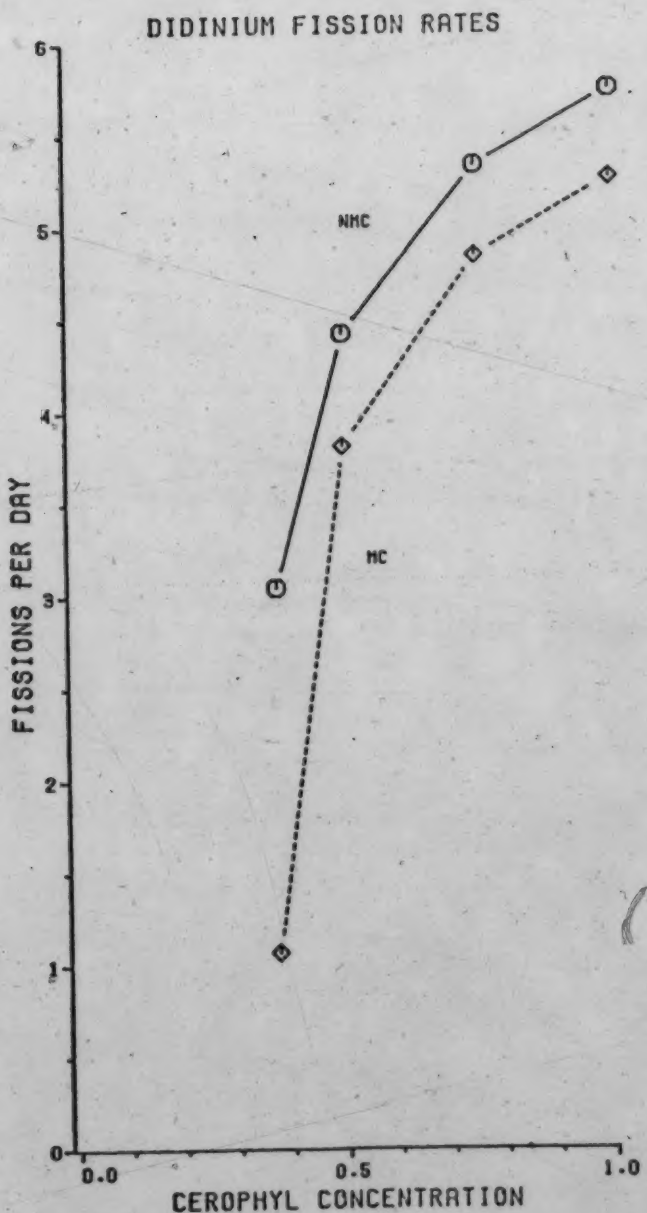

DIDINIUM FISSION RATES
FISSIONS PER DAY
CEROPHYL CONCENTRATION
NMC
MC
0
1
2
3
4
5
6
0.0
0.5
1.0

Figure 5a.

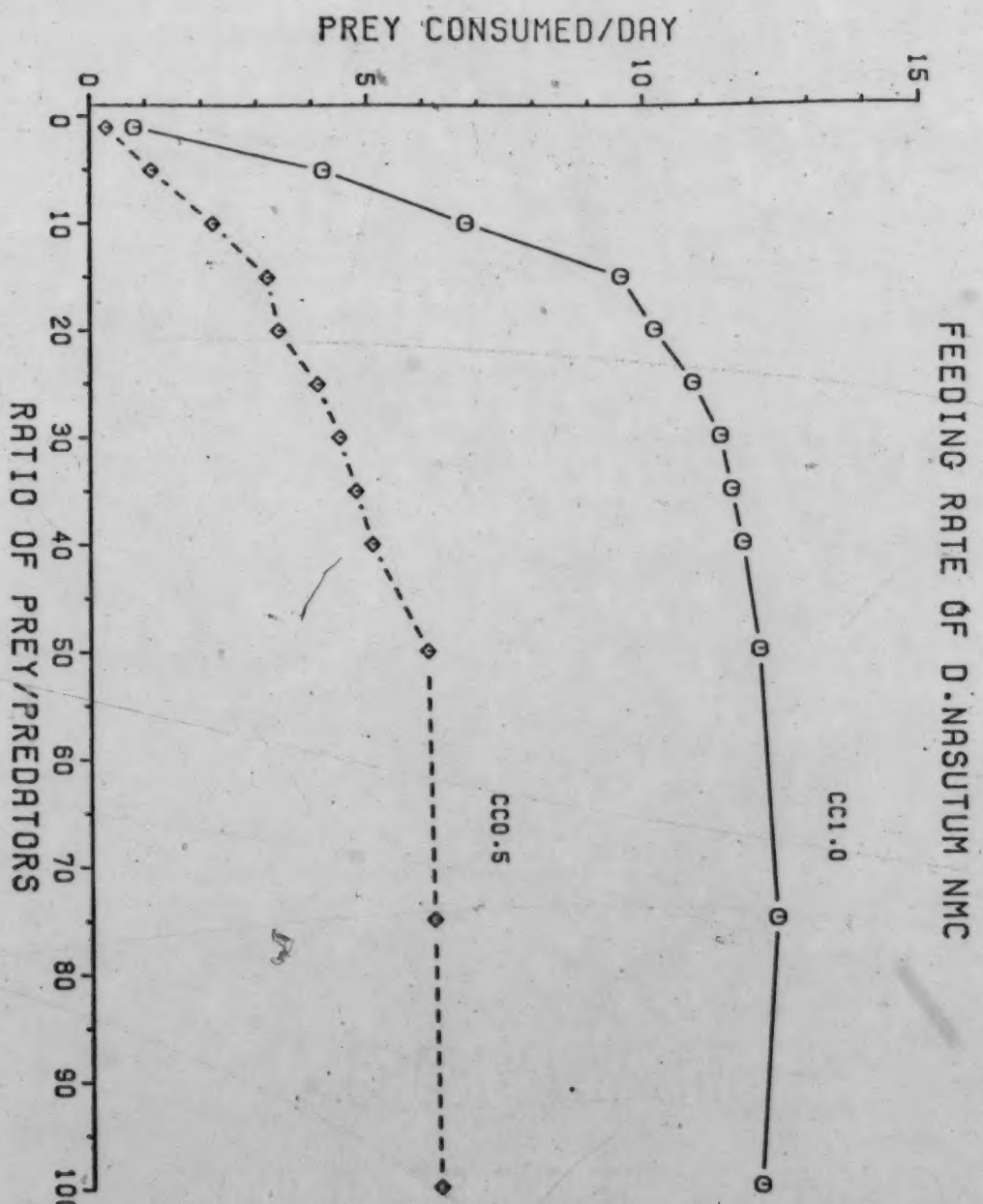

PREY CONSUMED/DAY
0
5
10
15
RATIO OF PREY/PREDATORS
0
10
20
30
40
50
60
70
80
90
100
CC1.0
CC0.5
FEEDING RATE OF D.NASUTUM NMC

Figure 5b.

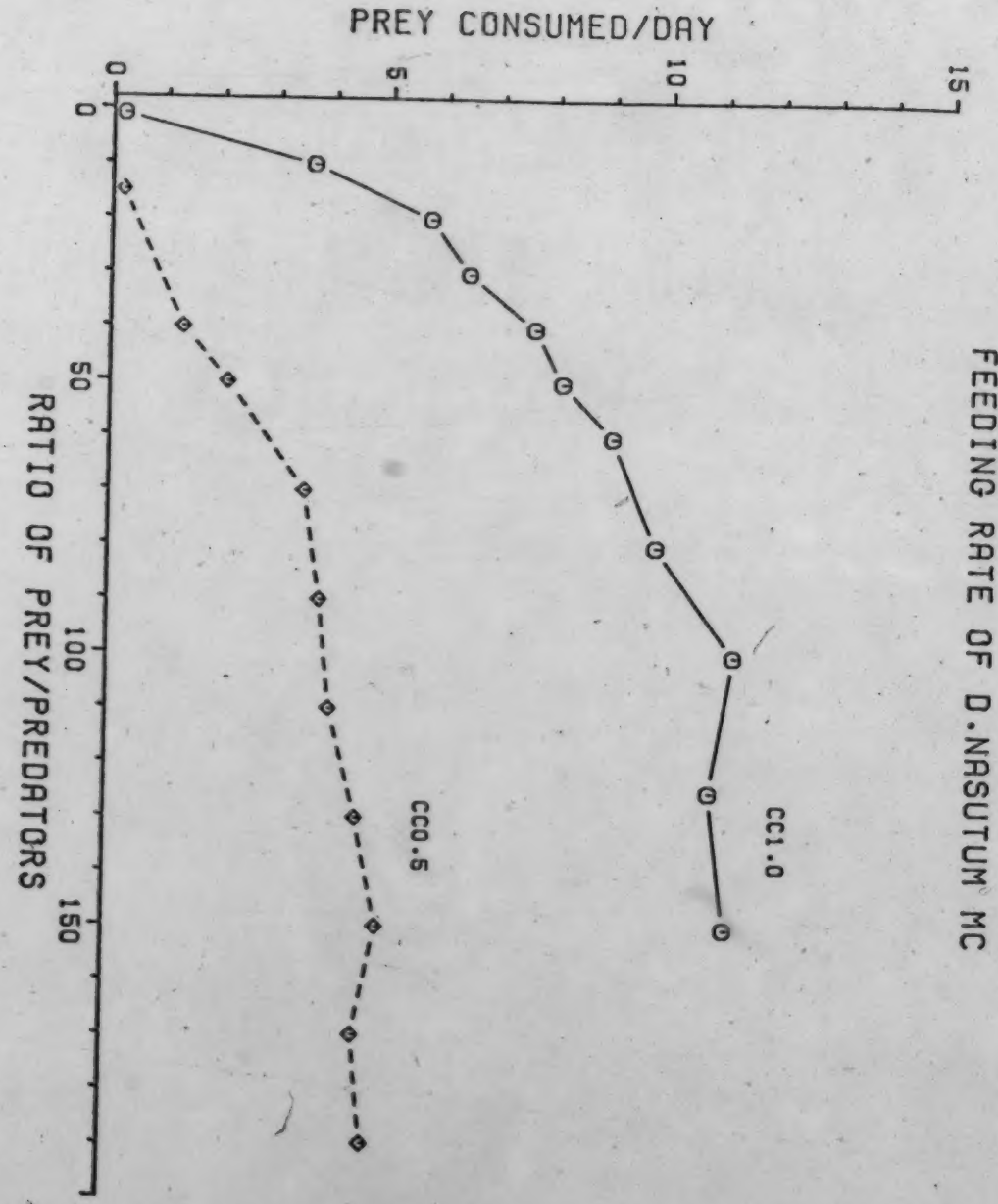

PREY CONSUMED/DAY
0
5
10
15
0
50
100
150
RATIO OF PREY/PREDATORS
CC0.5
CC1.0
FEEDING RATE OF D.NASUTUM MC

Figure 6.

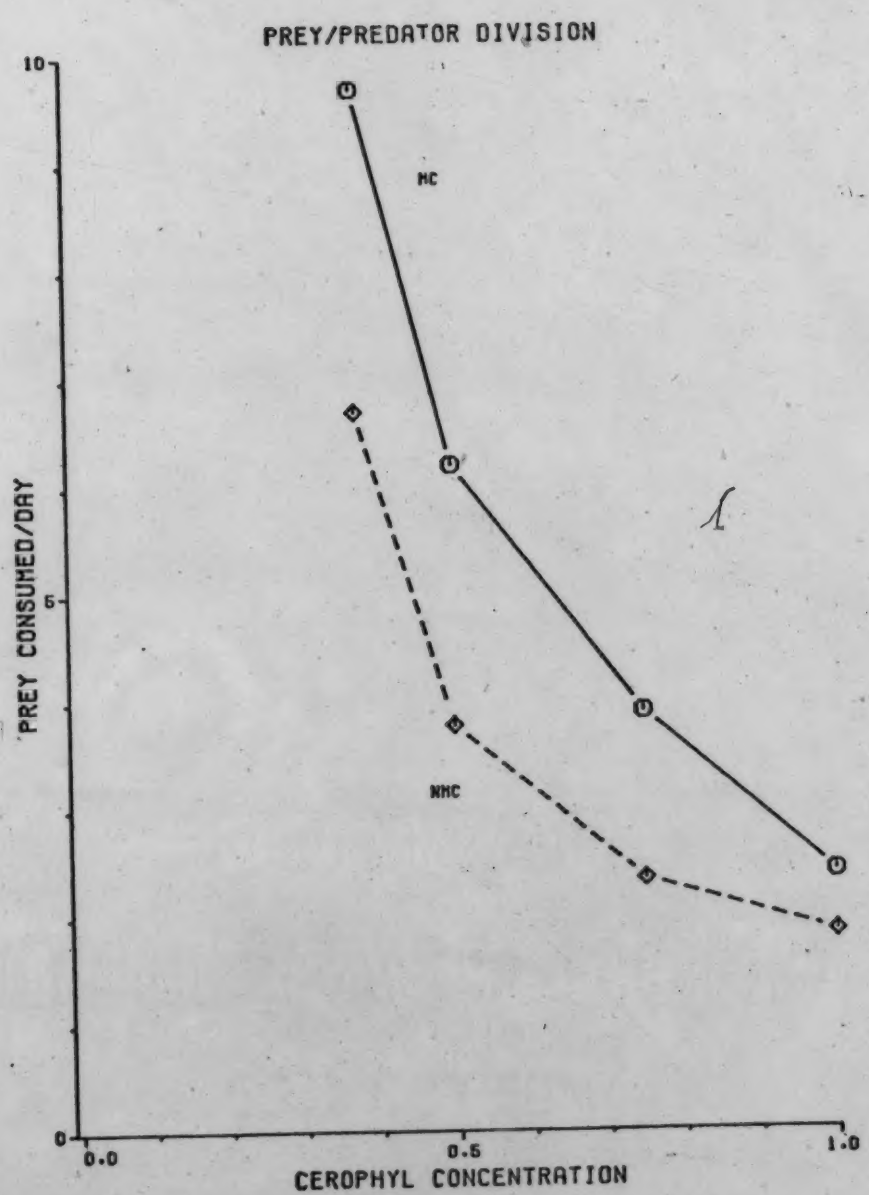

PREY/PREDATOR DIVISION
10
5
0
PREY CONSUMED/DAY
MC
NMC
0.0
0.5
1.0
CEROPHYL CONCENTRATION

Figure 7.

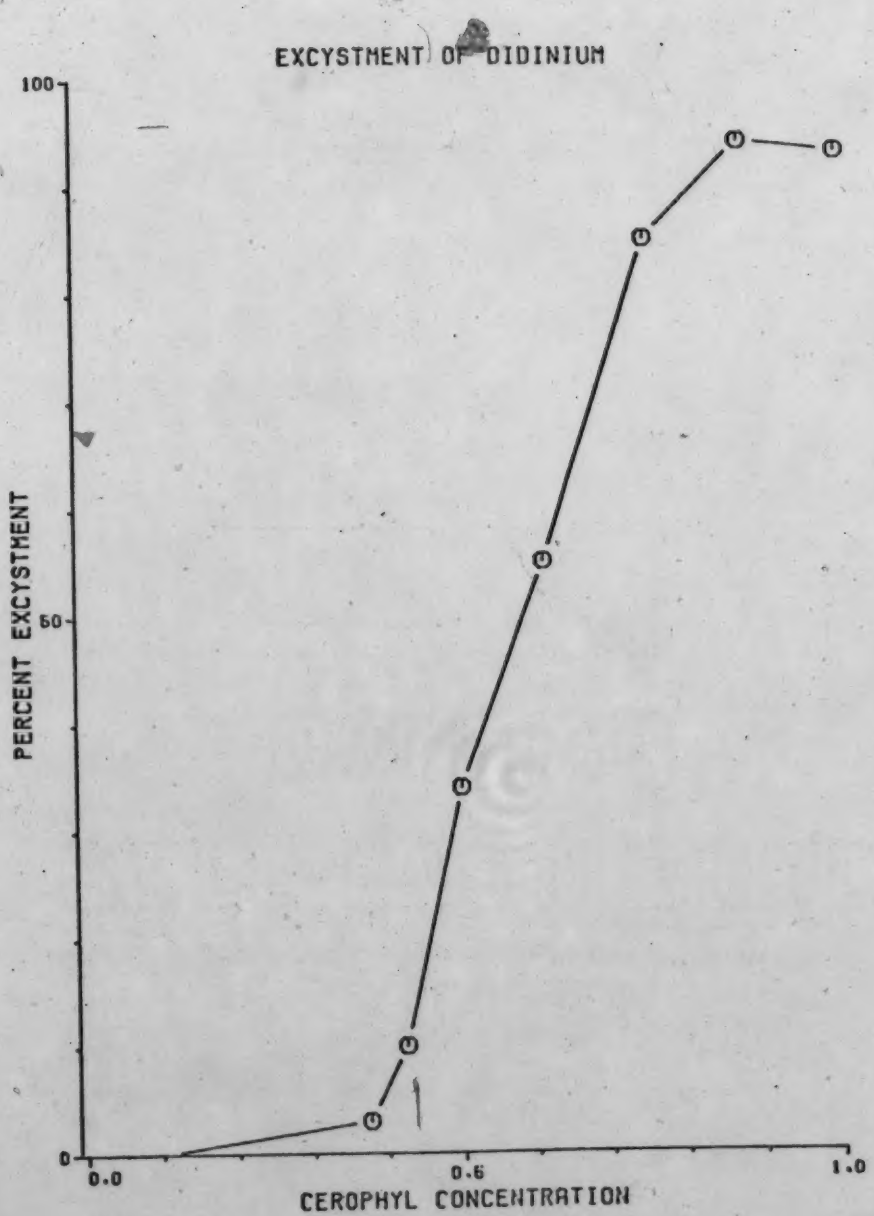

EXCYSTMENT OF DIDINIUM
100
50
0
PERCENT EXCYSTMENT
0.0
0.5
1.0
CEROPHYL CONCENTRATION

Figure 8.

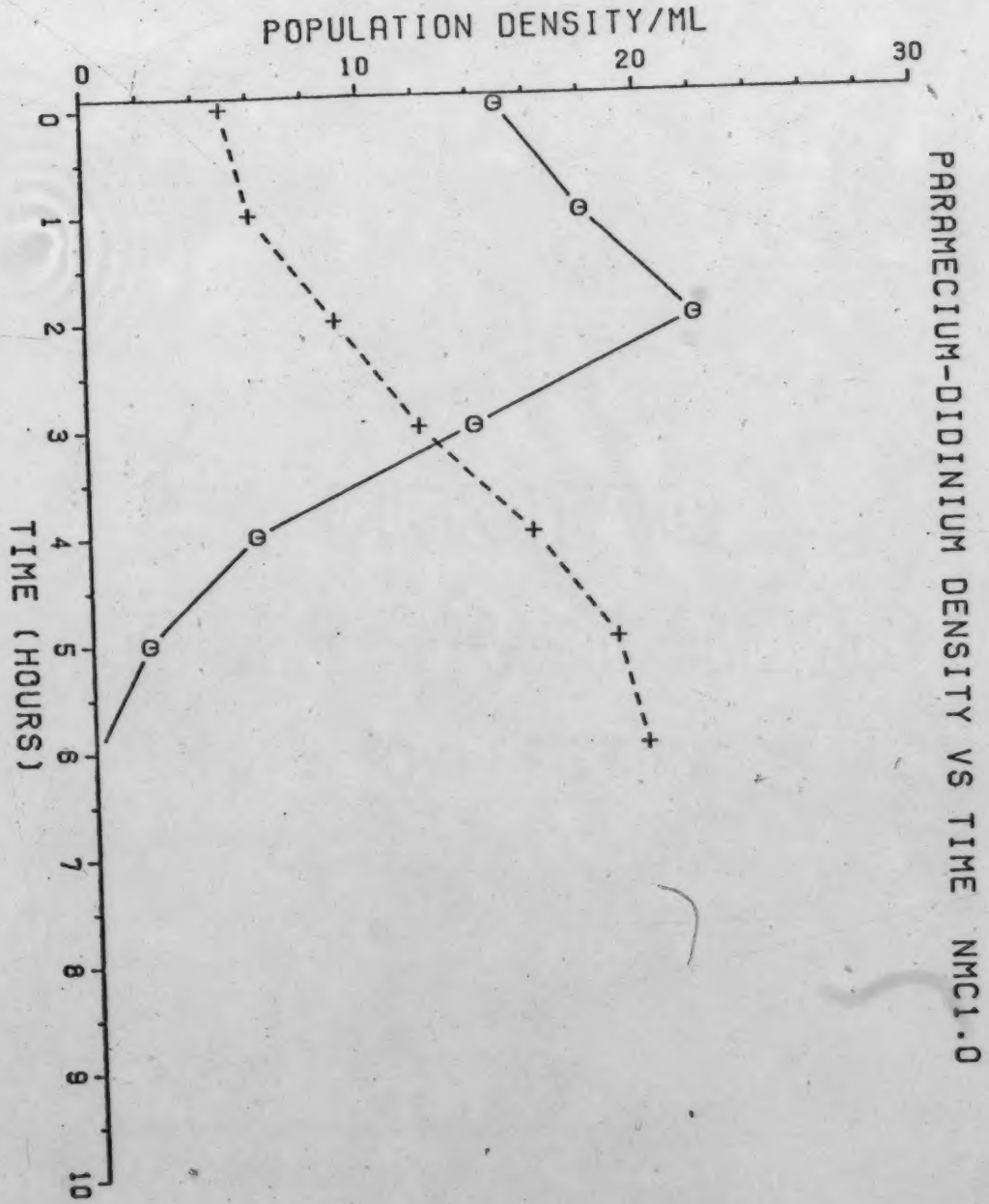

POPULATION DENSITY/ML
0
10
20
30
TIME (HOURS)
0
1
2
3
4
5
6
7
8
9
10
PARAMECIUM-DIDINIUM DENSITY VS TIME NMC1.0

Figure 9a.

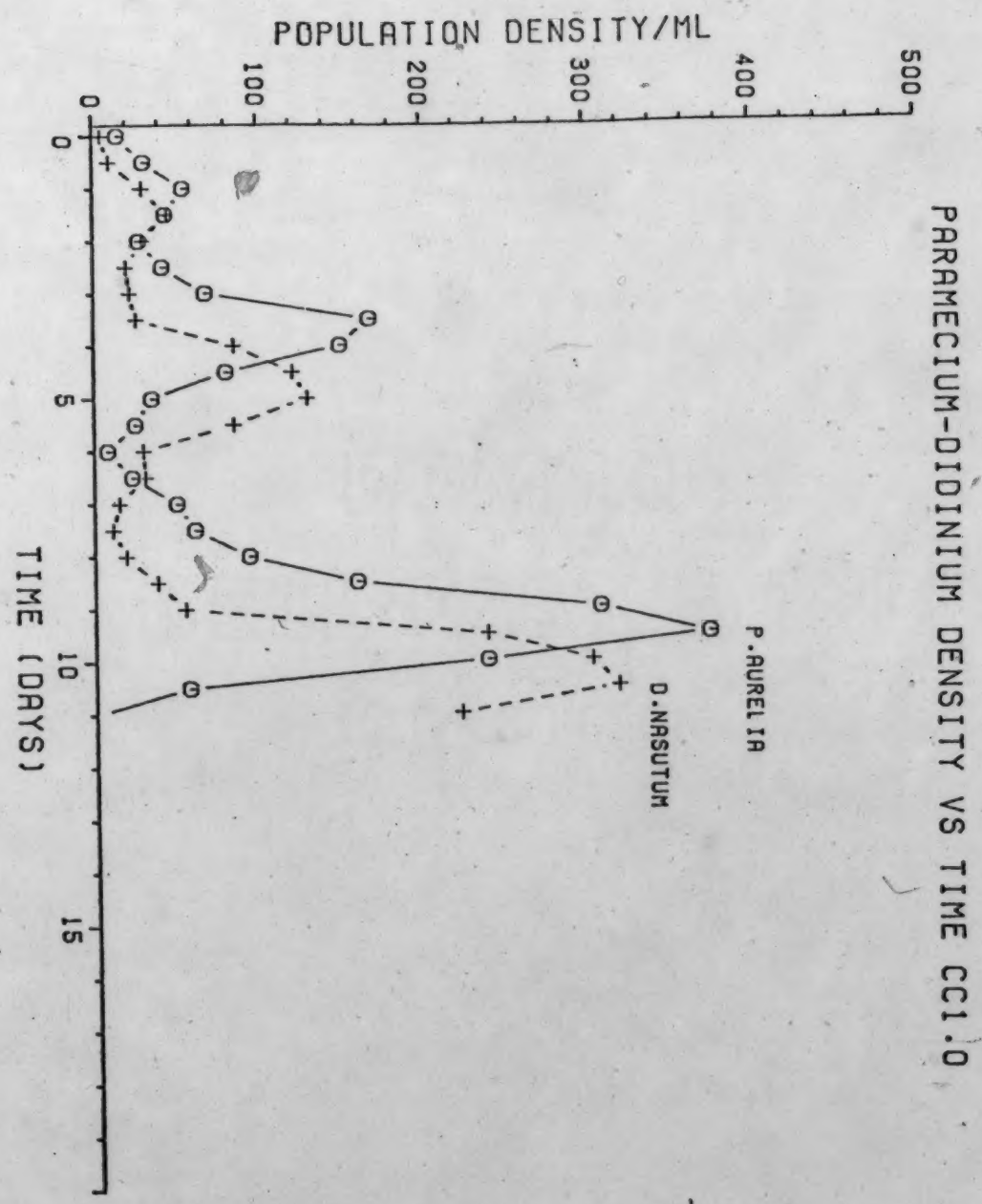

POPULATION DENSITY/ML
0
100
200
300
400
500
TIME (DAYS)
0
5
10
15
P.AURELIA
D.NASUTUM
PARAMECIUM-DIDINIUM DENSITY VS TIME CC1.0

Figure 9b.

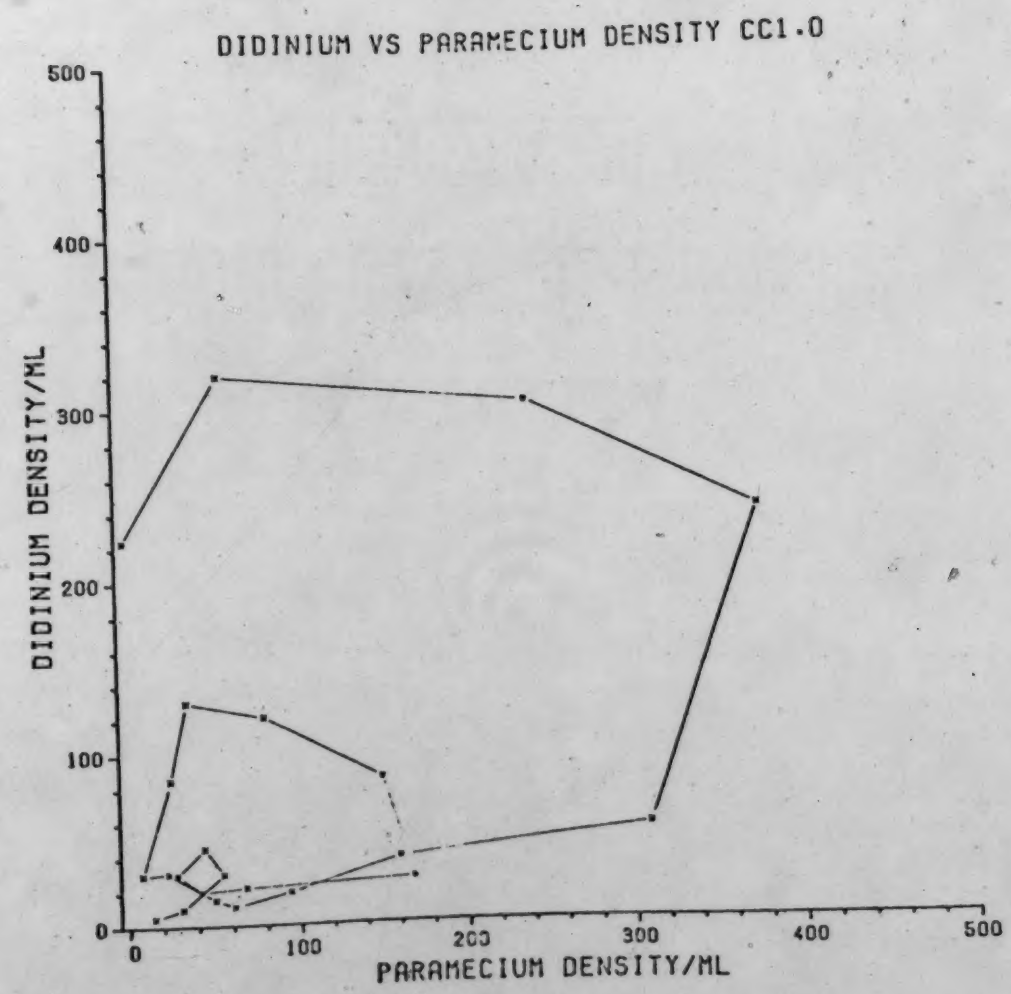

DIDINIUM VS PARAMECIUM DENSITY CC1.0
DIDINIUM DENSITY/ML
PARAMECIUM DENSITY/ML
0
100
200
300
400
500

Figure 10a.

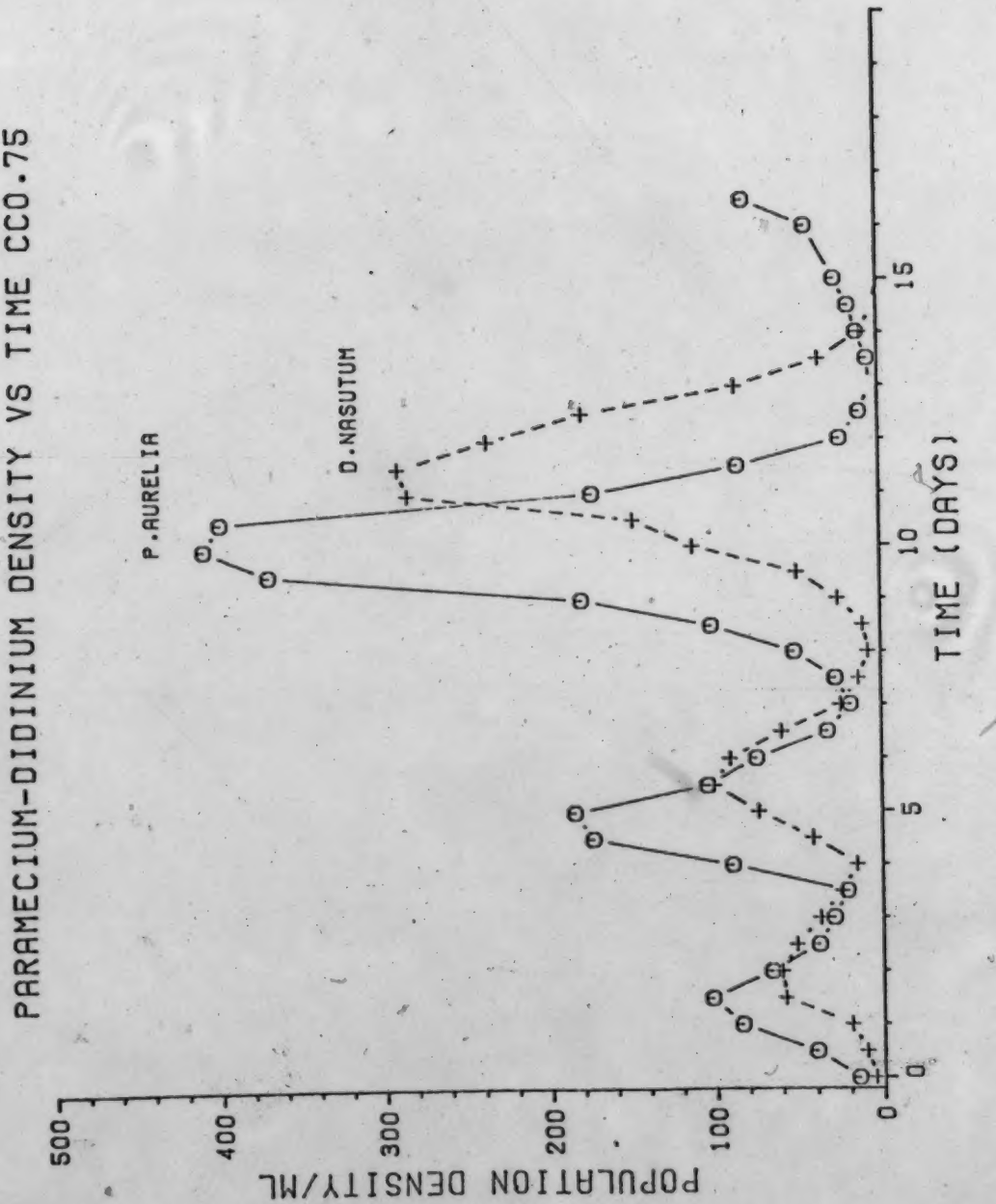

PARAMECIUM-DIDINIUM DENSITY VS TIME CCO.75
P.AURELIA
D.NASUTUM
POPULATION DENSITY/ML
TIME (DAYS)
0
100
200
300
400
500
5
10
15

Figure 10b.

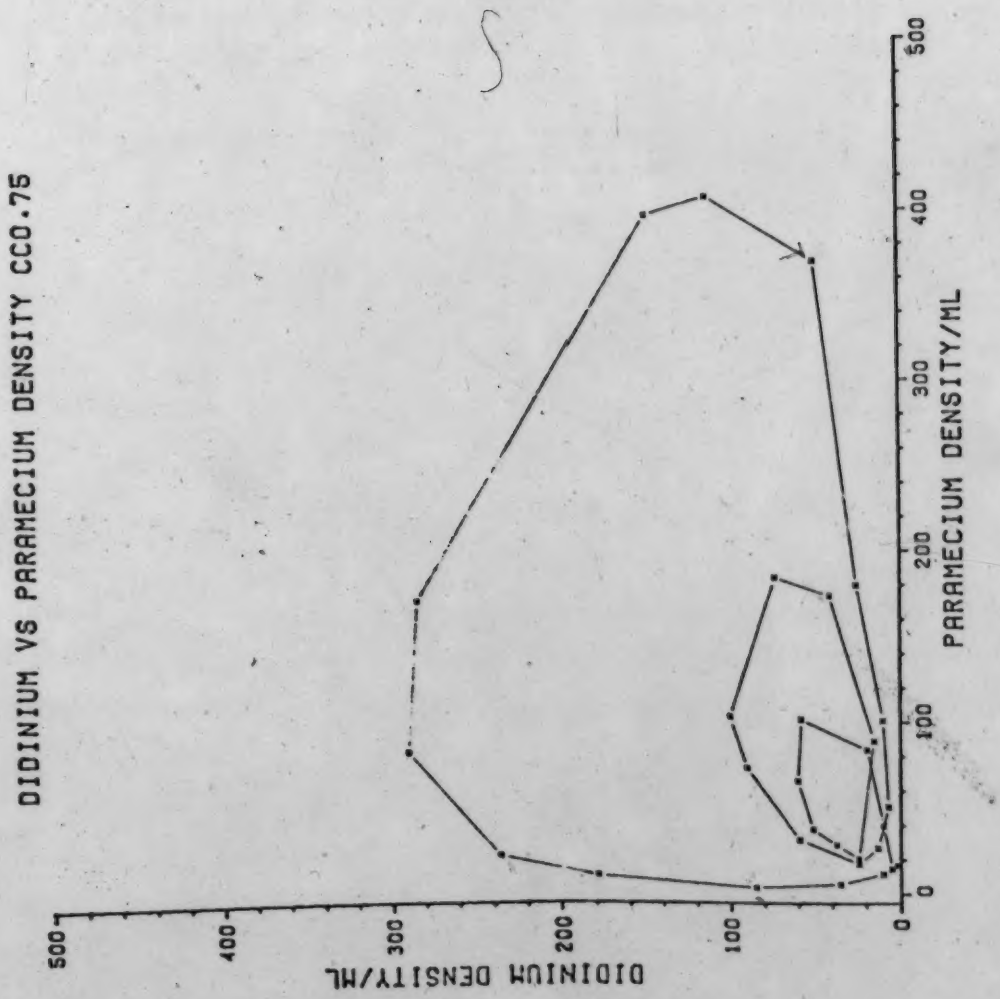

DIDINIUM VS PARAMECIUM DENSITY CCO.75
DIDINIUM DENSITY/ML
PARAMECIUM DENSITY/ML
0
100
200
300
400
500

Figure 11a.

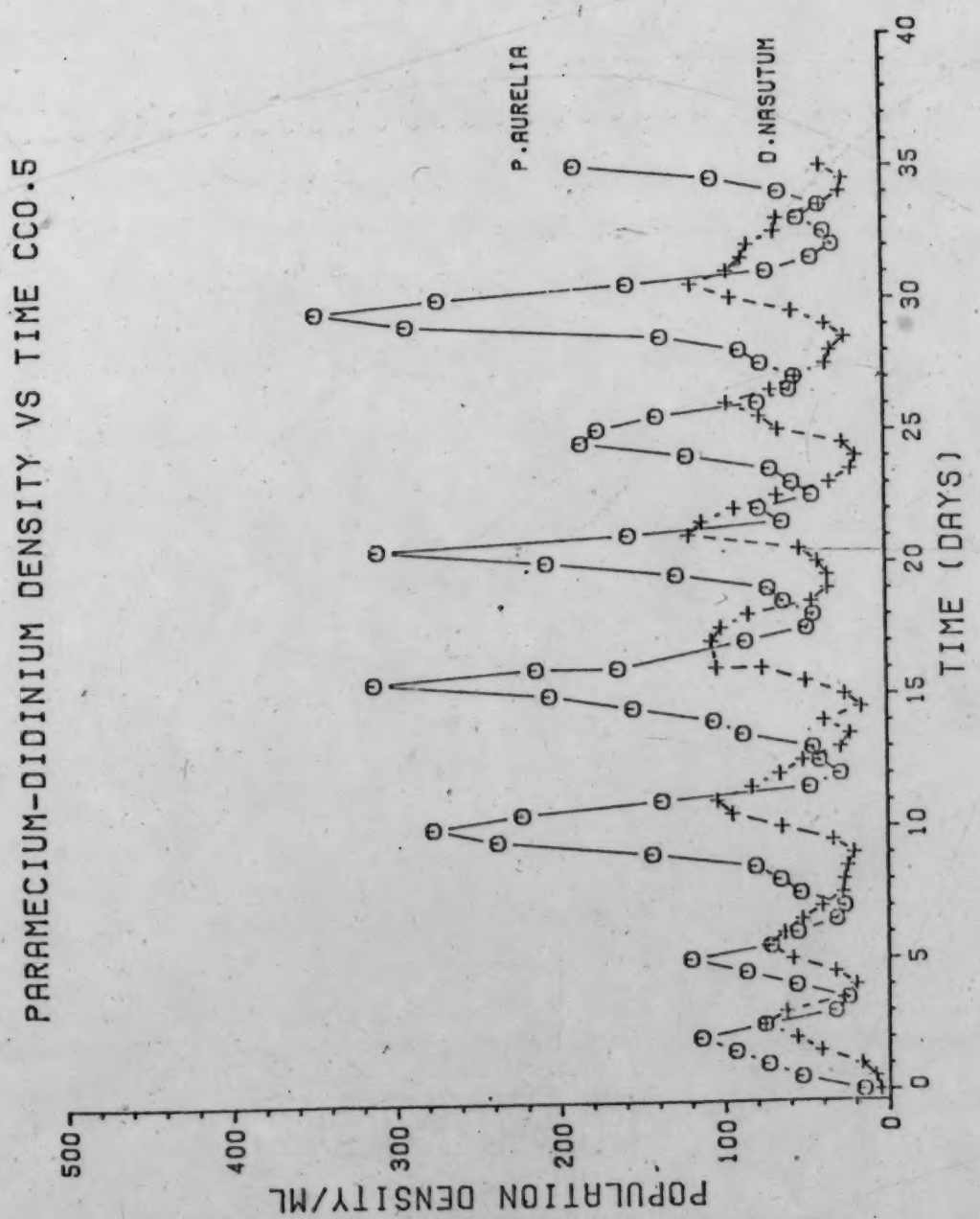

PARAMECIUM-DIDINIUM DENSITY VS TIME CCO.5
P.AURELIA
D.NASUTUM
POPULATION DENSITY/ML
TIME (DAYS)
0
100
200
300
400
500
0
5
10
15
20
25
30
35
40

Figure 11b.

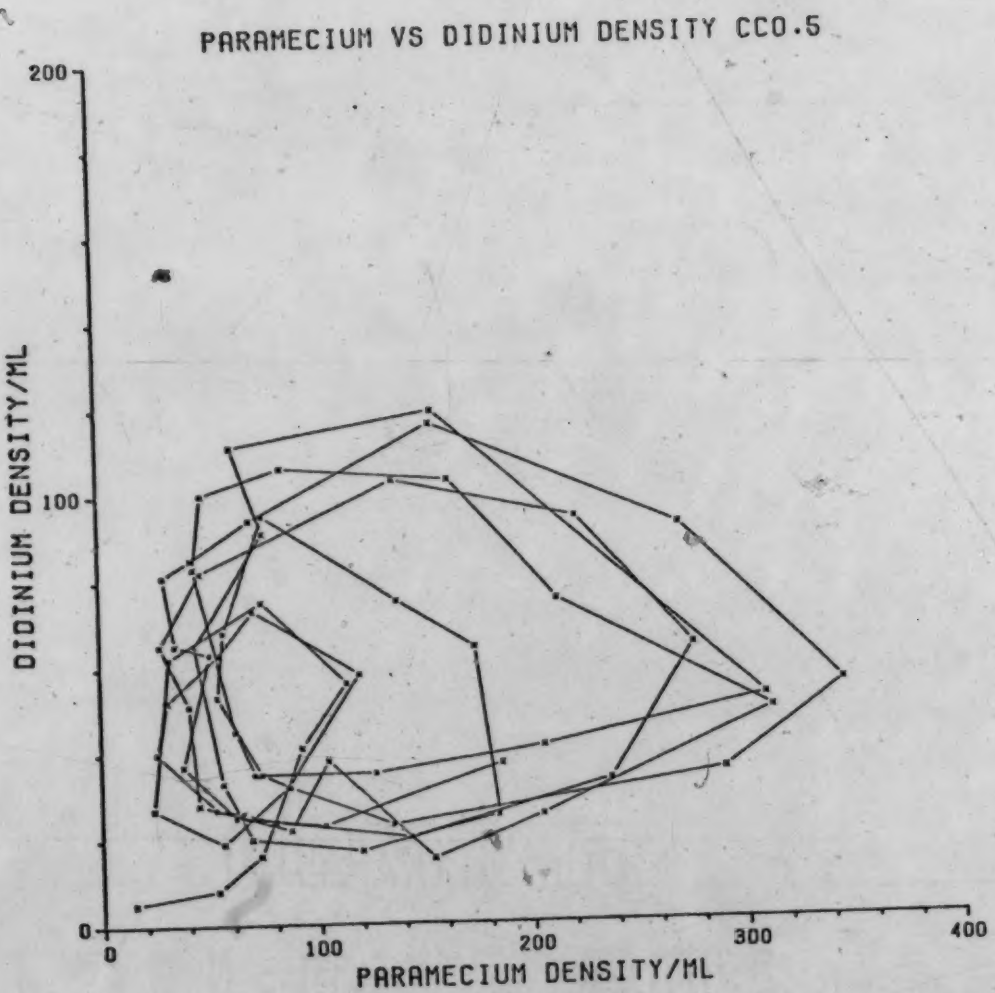

PARAMECIUM VS DIDINIUM DENSITY CC0.5
DIDINIUM DENSITY/ML
200
100
0
0
100
200
300
400
PARAMECIUM DENSITY/ML

Figure 12a.

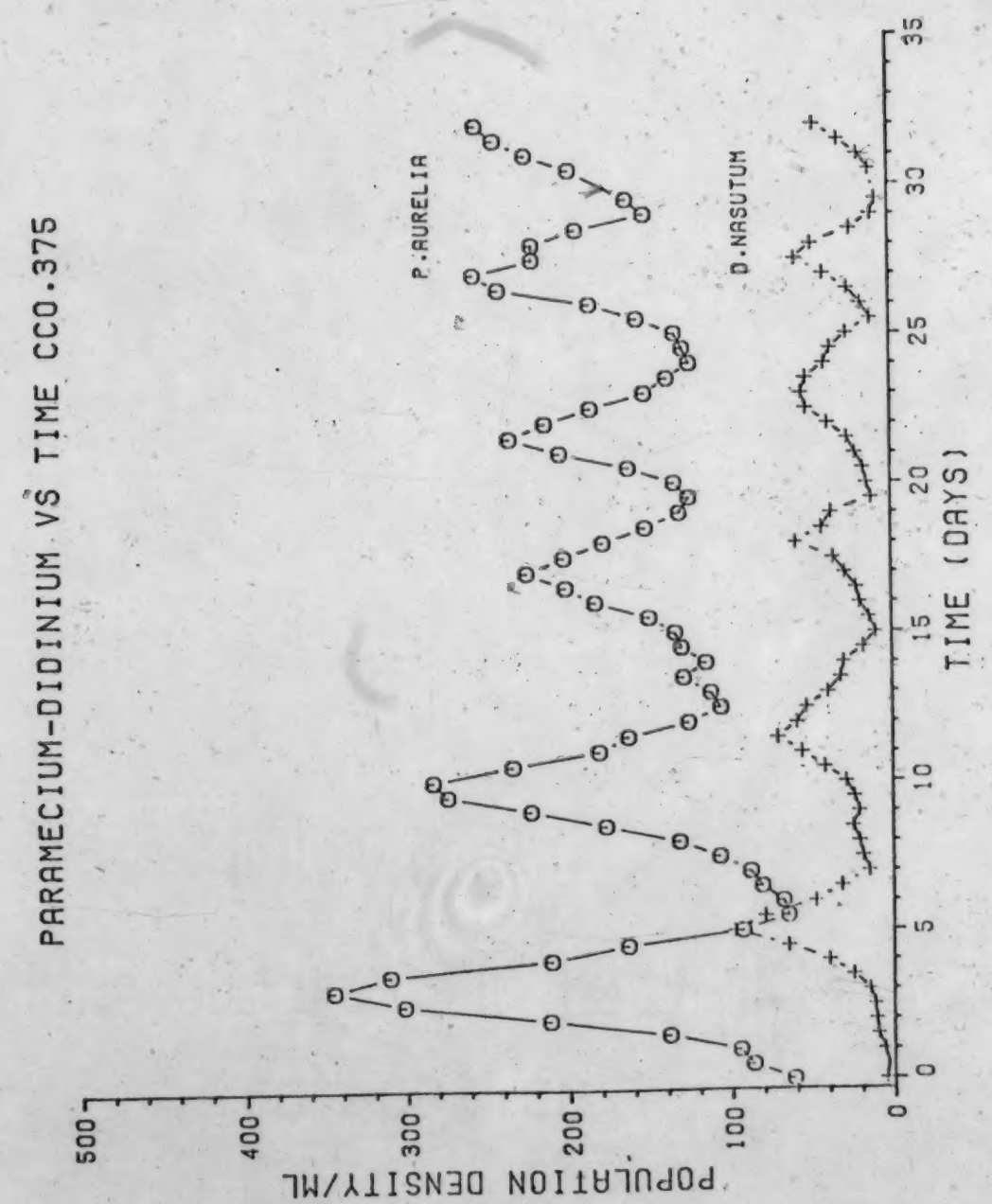

PARAMECIUM-DIDINIUM VS TIME CCO.375
P.AURELIA
D.NASUTUM
POPULATION DENSITY/ML
TIME (DAYS)
0
100
200
300
400
500
0
5
10
15
20
25
30
35

Figure 12b.

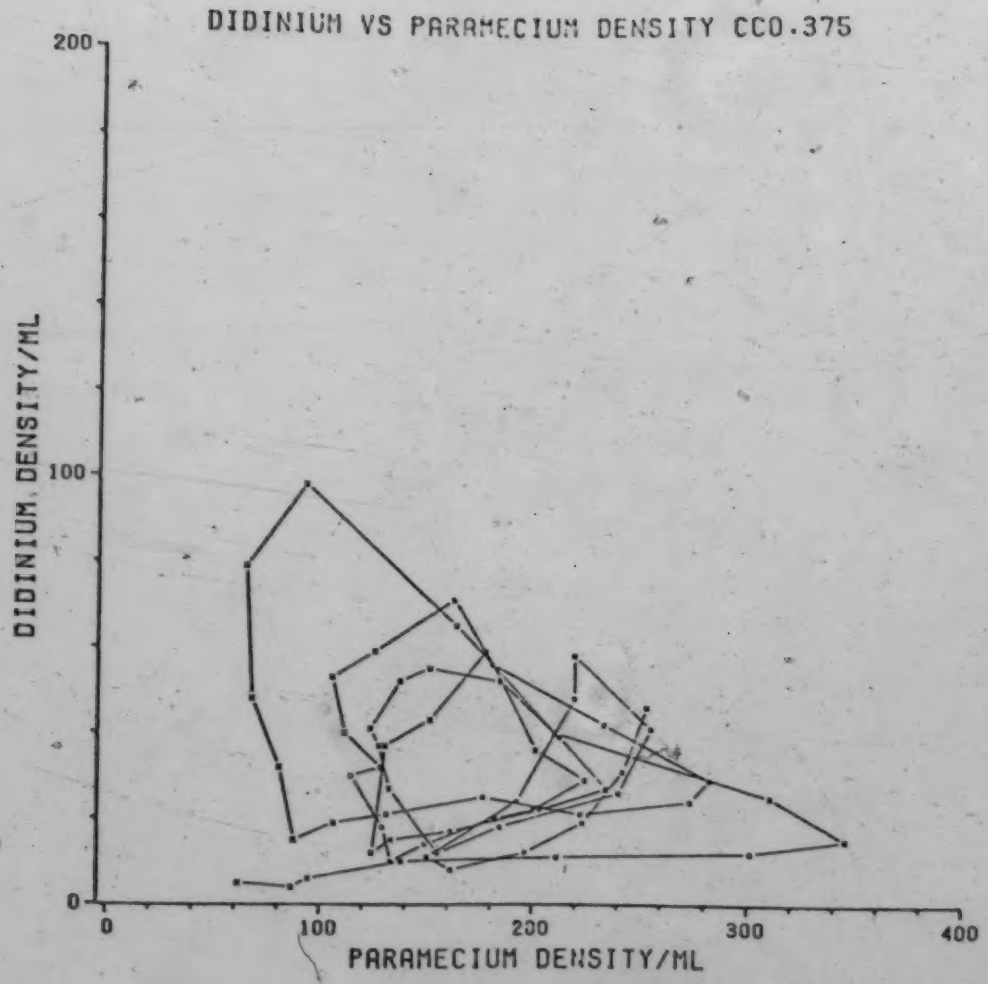

DIDINIUM VS PARAMECIUM DENSITY CCO.375
DIDINIUM DENSITY/ML
200
100
0
0
100
200
300
400
PARAMECIUM DENSITY/ML

Figure 13.

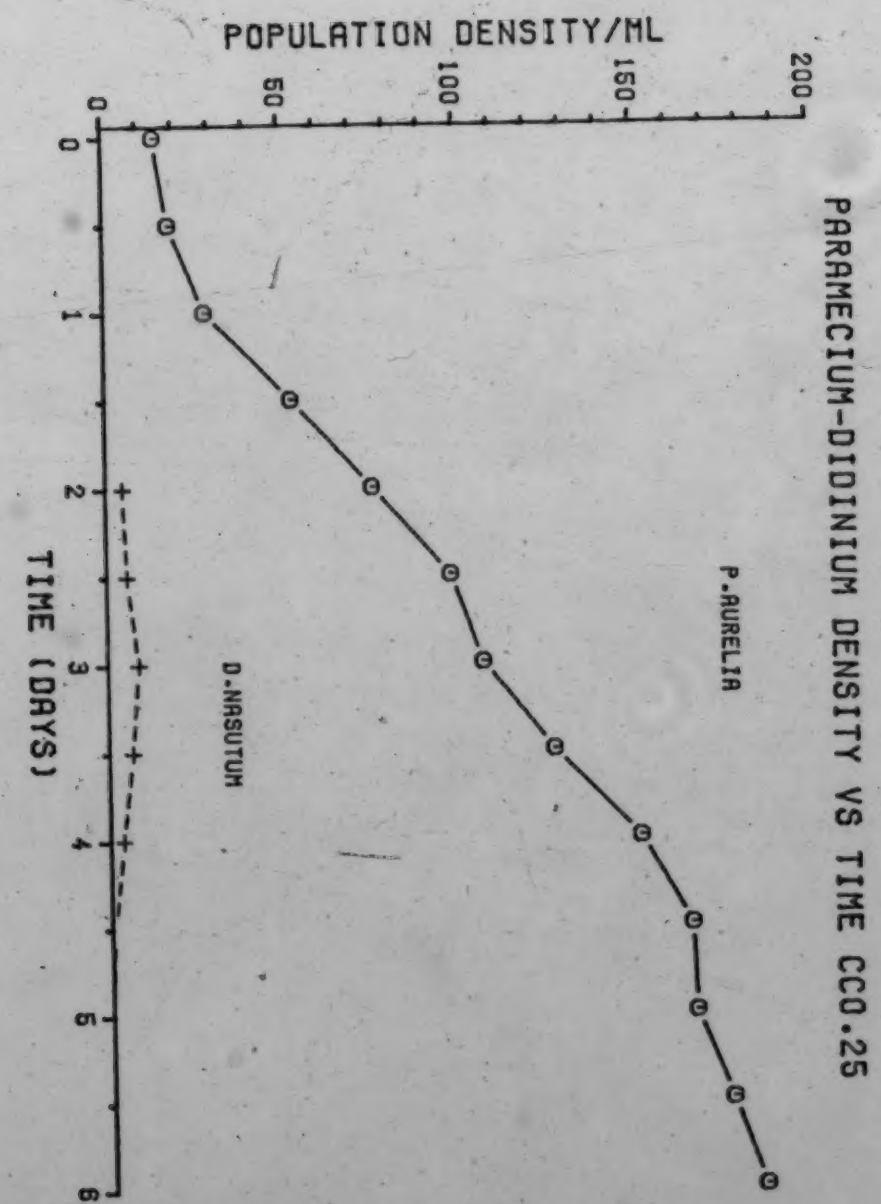

POPULATION DENSITY/ML
0
50
100
150
200
TIME (DAYS)
0
1
2
3
4
5
6
P.AURELIA
D.NASUTUM
PARAMECIUM-DIDINIUM DENSITY VS TIME CCO.25

Figure 14a.

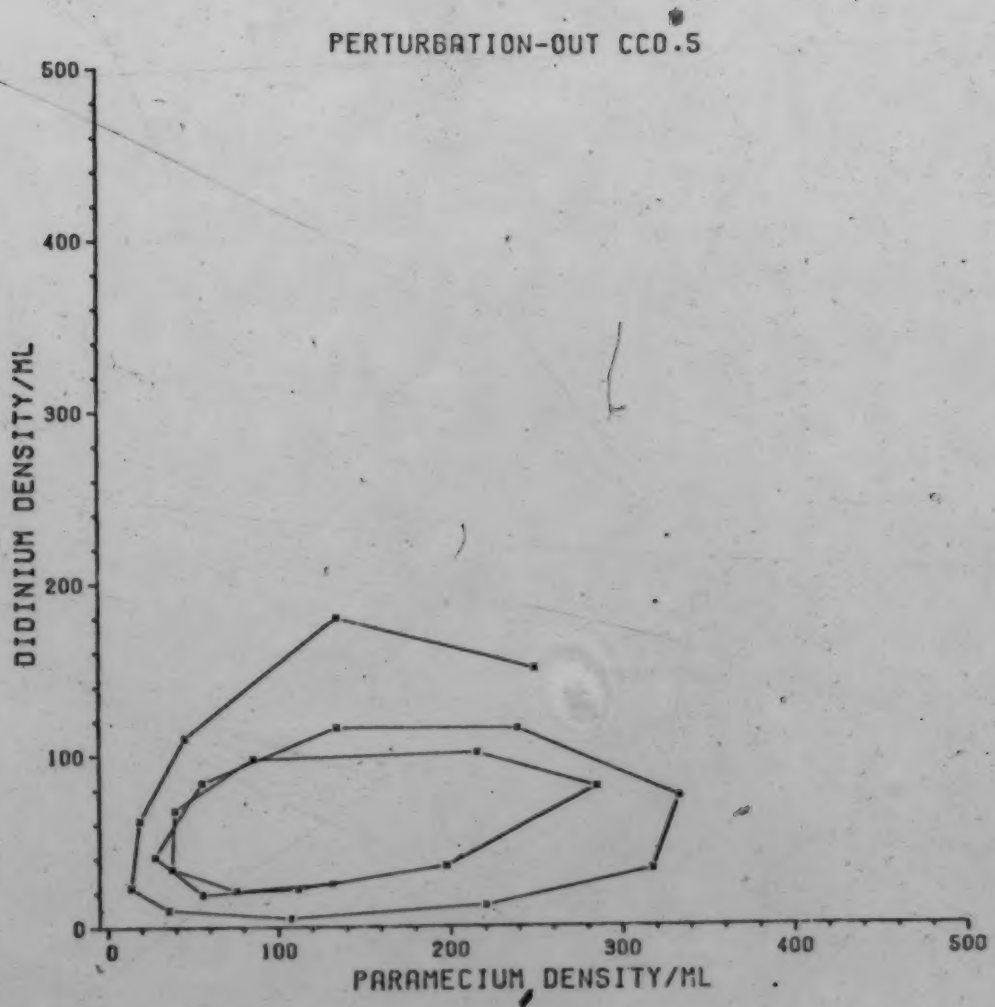

PERTURBATION-OUT CC0.5
DIDINIUM DENSITY/ML
PARAMECIUM DENSITY/ML
0
100
200
300
400
500

Figure 14b.

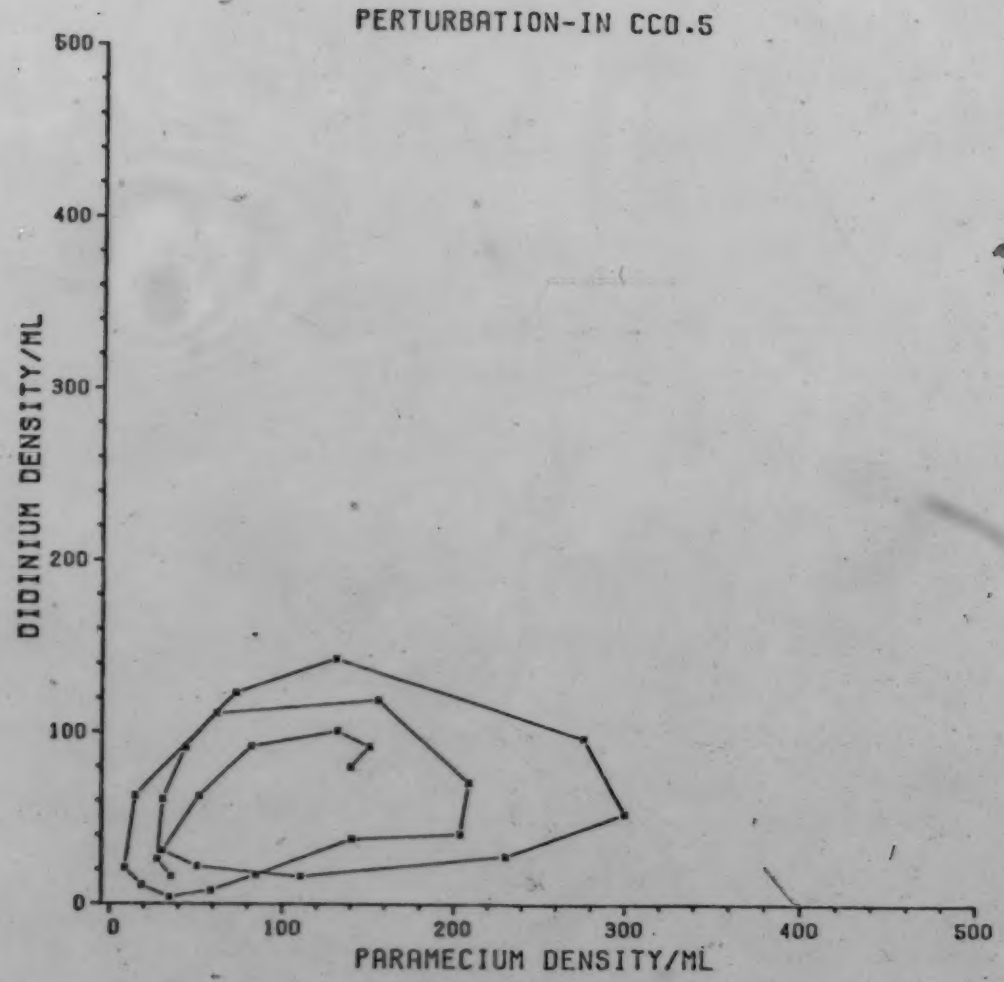

PERTURBATION-IN CCO.5
DIDINIUM DENSITY/ML
PARAMECIUM DENSITY/ML
0
100
200
300
400
500

Figure 14c.

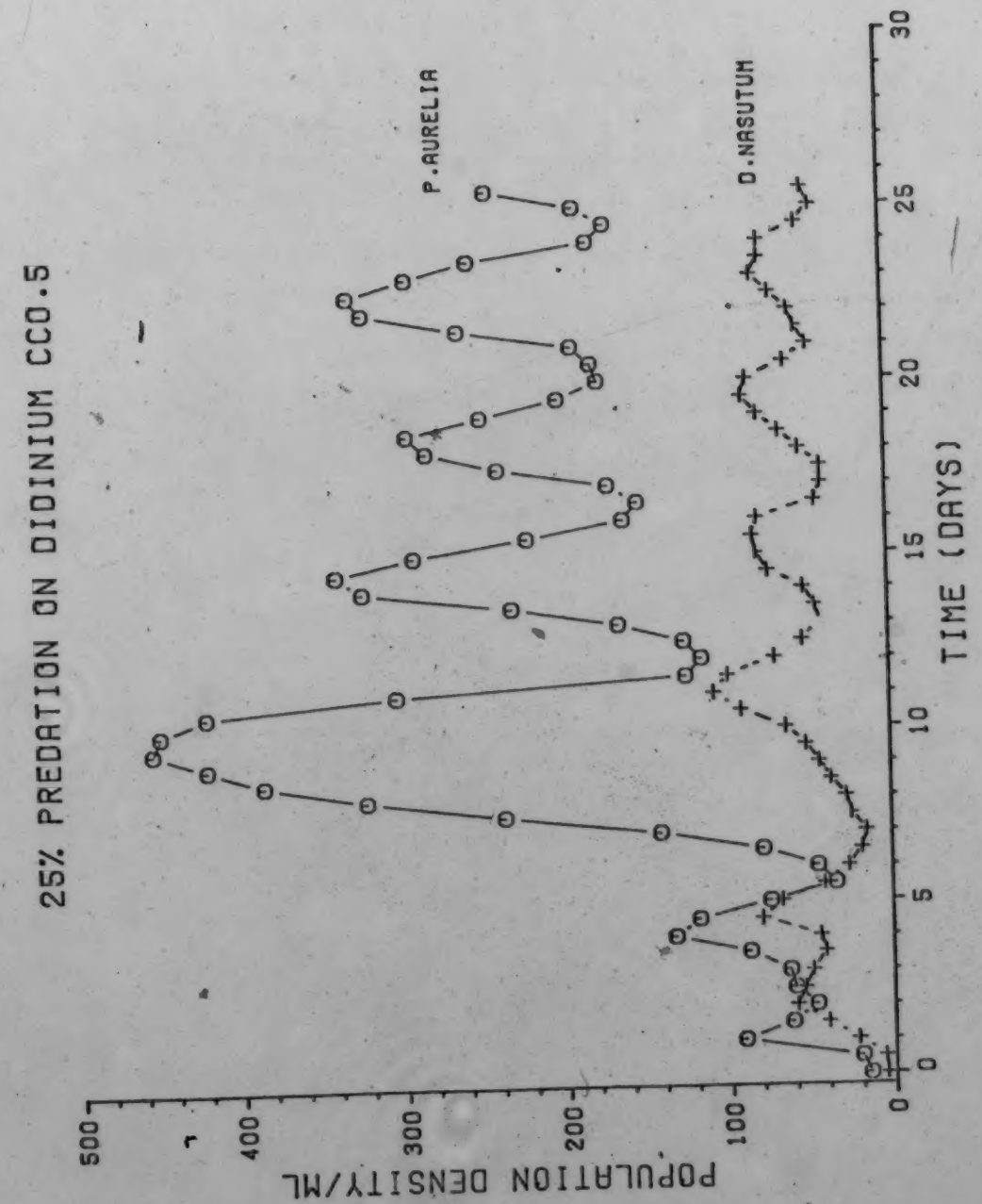

25% PREDATION ON DIDINIUM CCO.5
P.AURELIA
D.NASUTUM
POPULATION DENSITY/ML
TIME (DAYS)
0
100
200
300
400
500
0
5
10
15
20
25
30

Figure 15a.

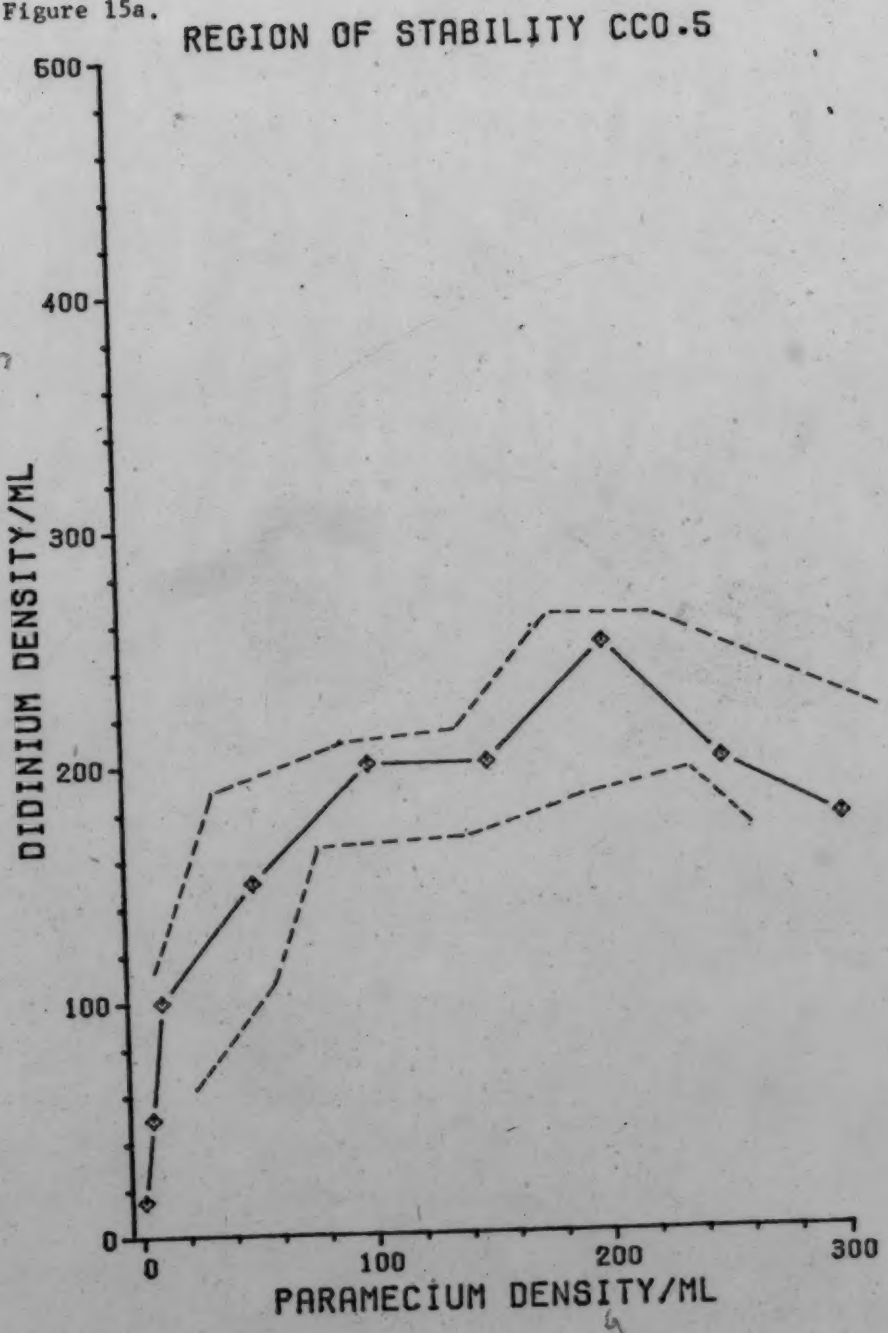

REGION OF STABILITY CCO.5
600
400
300
200
100
0
DIDINIUM DENSITY/ML
0
100
200
300
PARAMECIUM DENSITY/ML

Figure 15b.

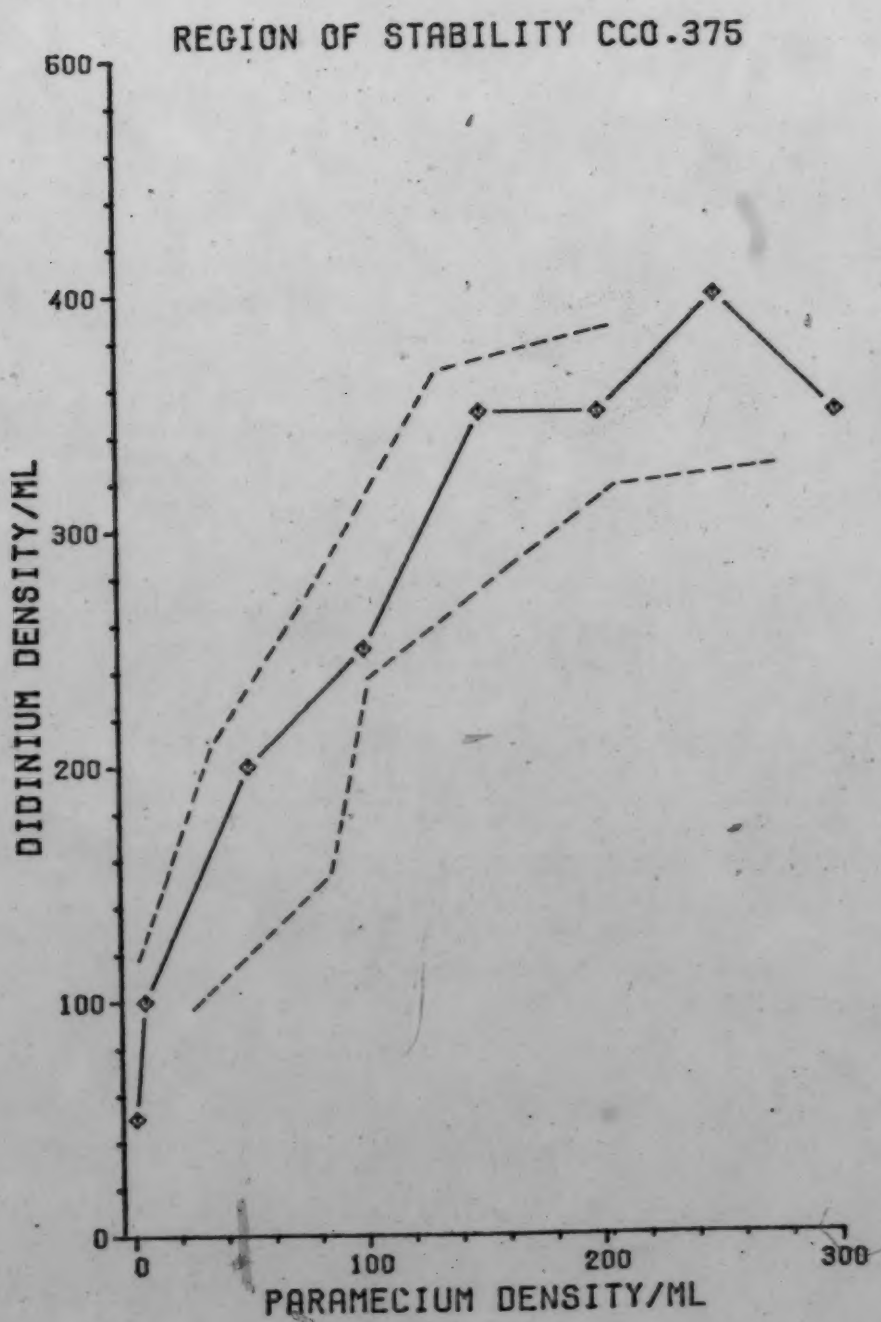

REGION OF STABILITY CCO.375
600
400
300
200
100
0
DIDINIUM DENSITY/ML
0
100
200
300
PARAMECIUM DENSITY/ML

Figure 16a.

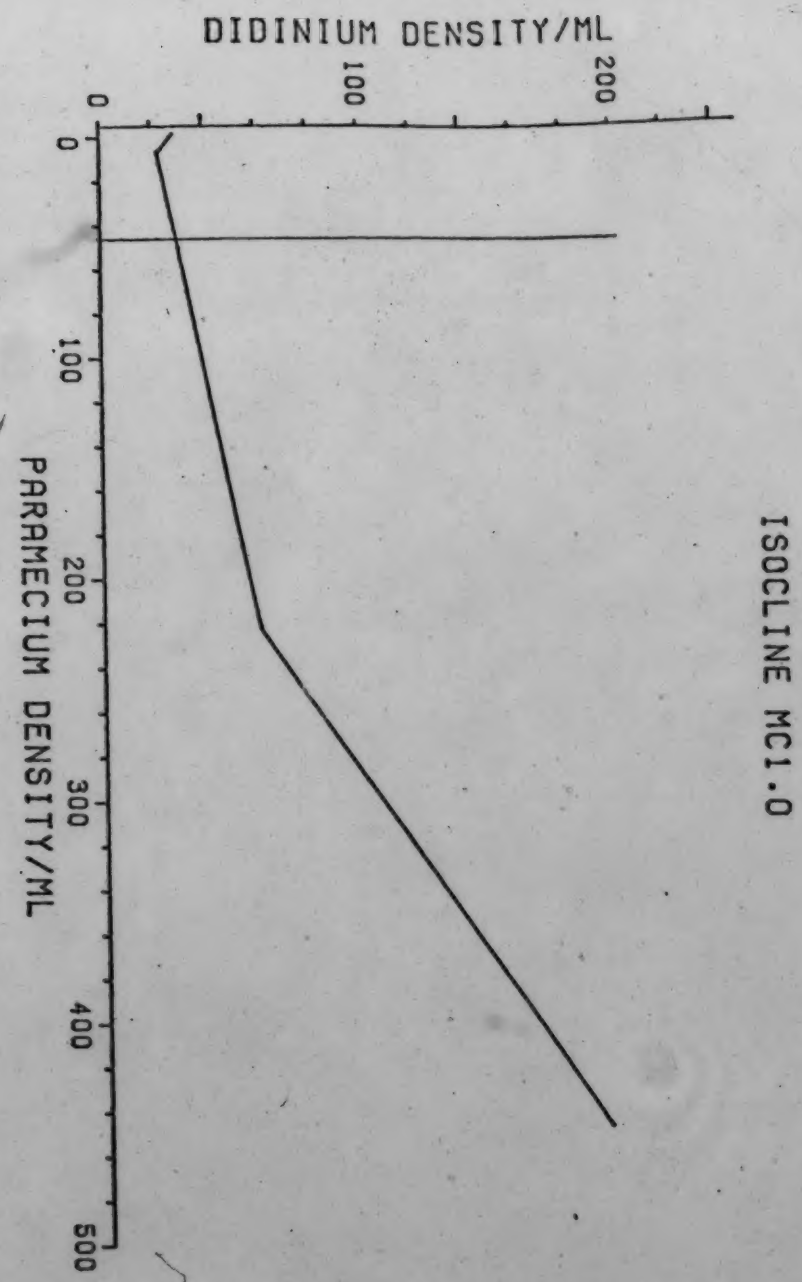

DIDINIUM DENSITY/ML
0
100
200
PARAMECIUM DENSITY/ML
0
100
200
300
400
500
ISOCLINE MC1.0

Figure 16b.

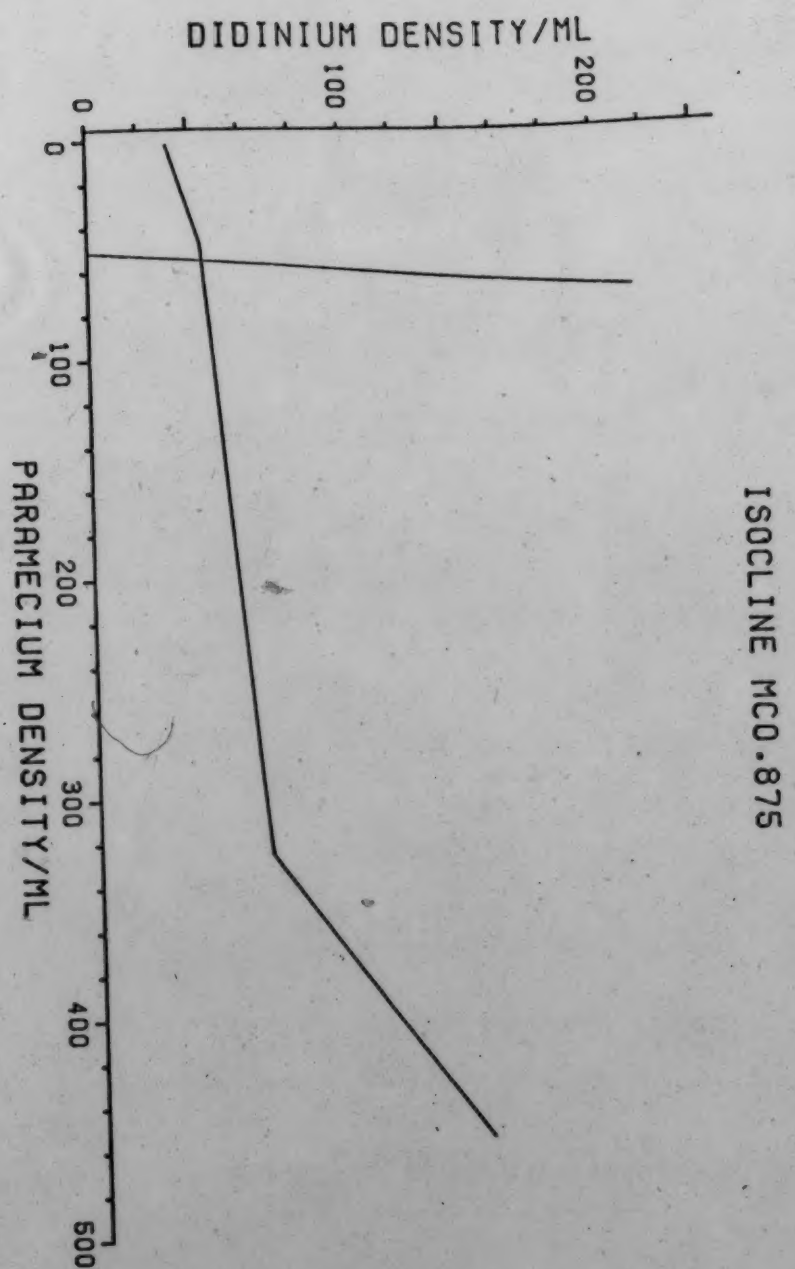

DIDINIUM DENSITY/ML
0
100
200
0
100
200
300
400
500
PARAMECIUM DENSITY/ML
ISOCLINE MCO·875

Figure 16c.

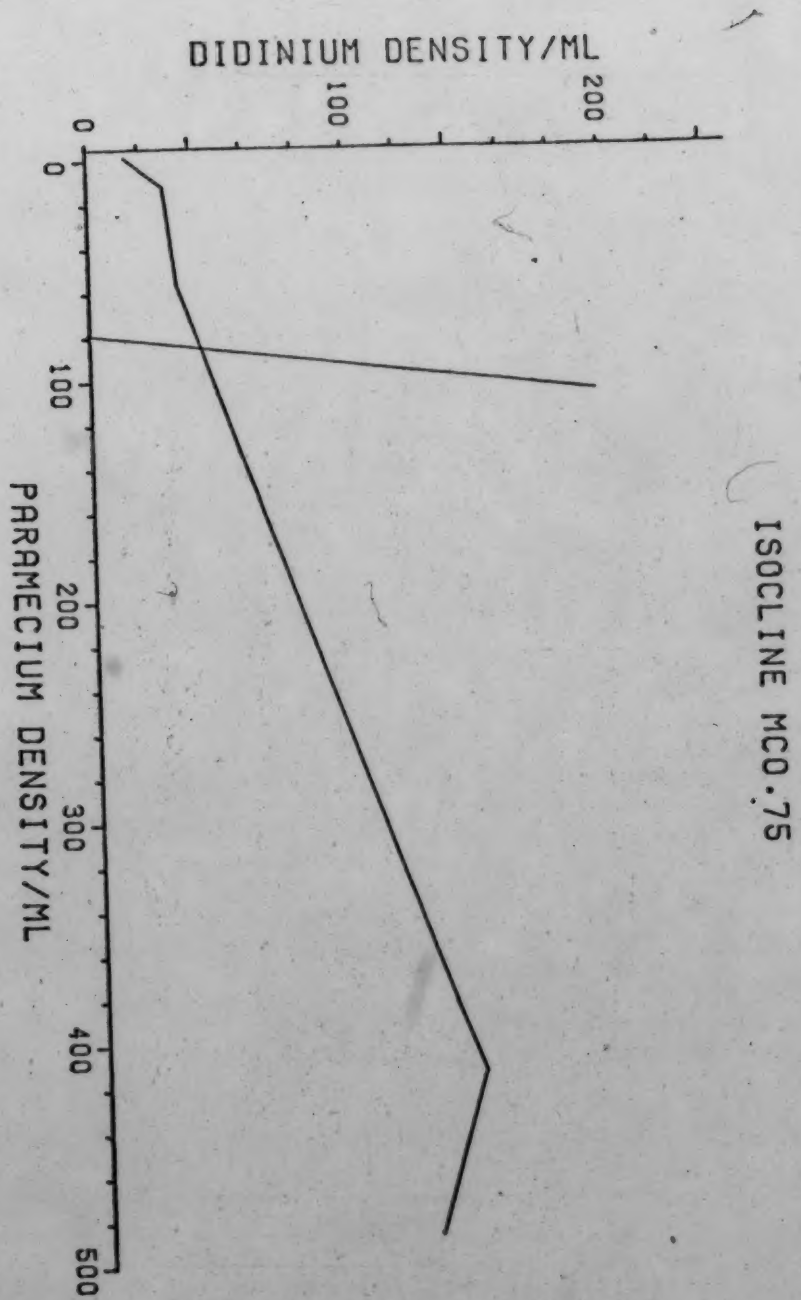

DIDINIUM DENSITY/ML
0
100
200
0
100
200
300
400
500
PARAMECIUM DENSITY/ML
ISOCLINE MCO.75

Figure 16d.

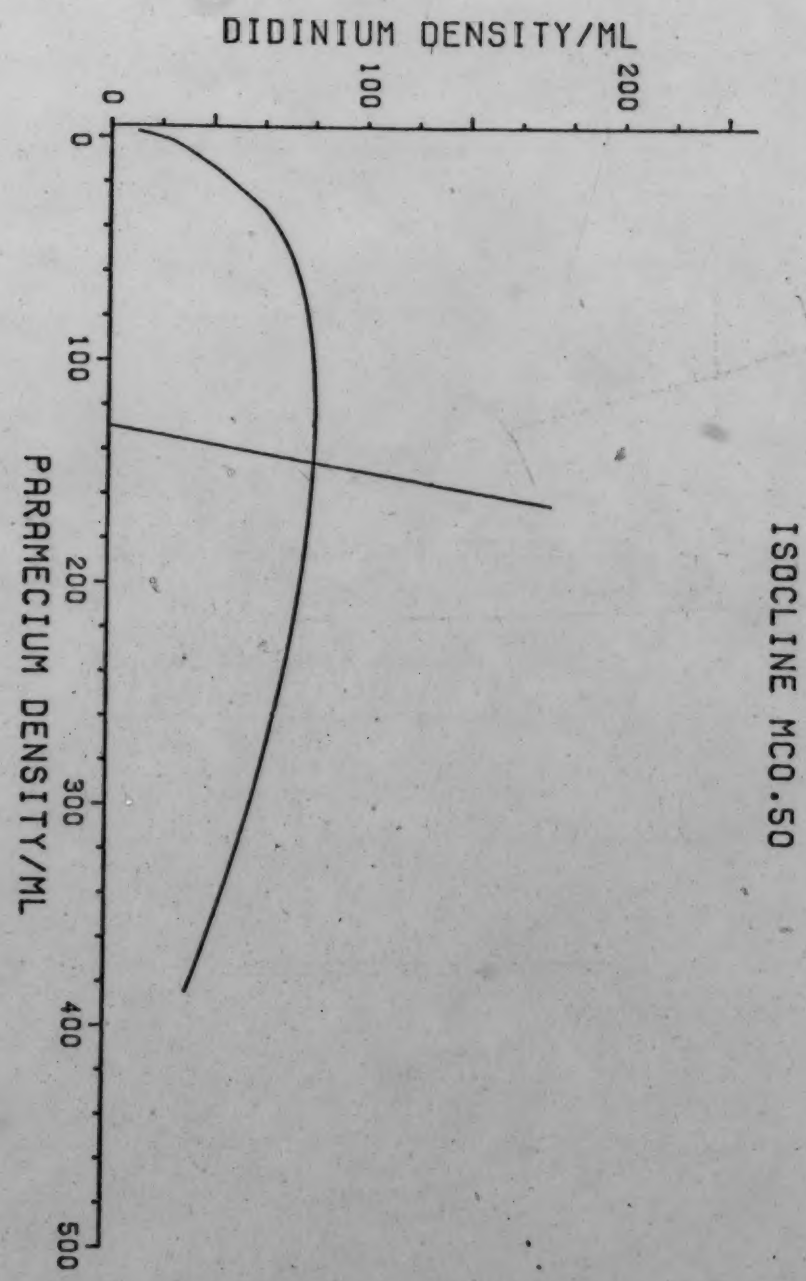

DIDINIUM DENSITY/ML
0
100
200
0
100
200
300
400
500
PARAMECIUM DENSITY/ML
ISOCLINE MCO.50

Figure 16e.

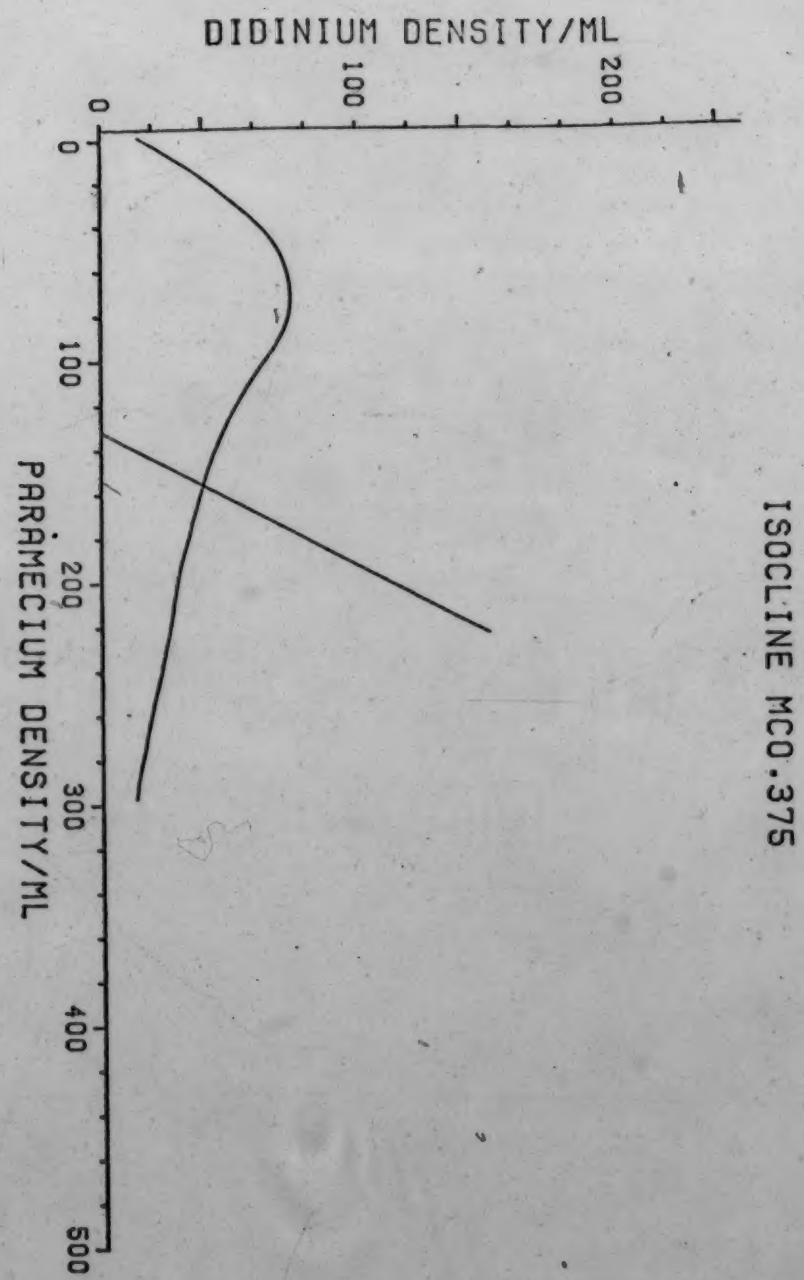

DIDINIUM DENSITY/ML
0
100
200
PARAMECIUM DENSITY/ML
0
100
200
300
400
500
ISOCLINE MCO.375

Figure 17a.

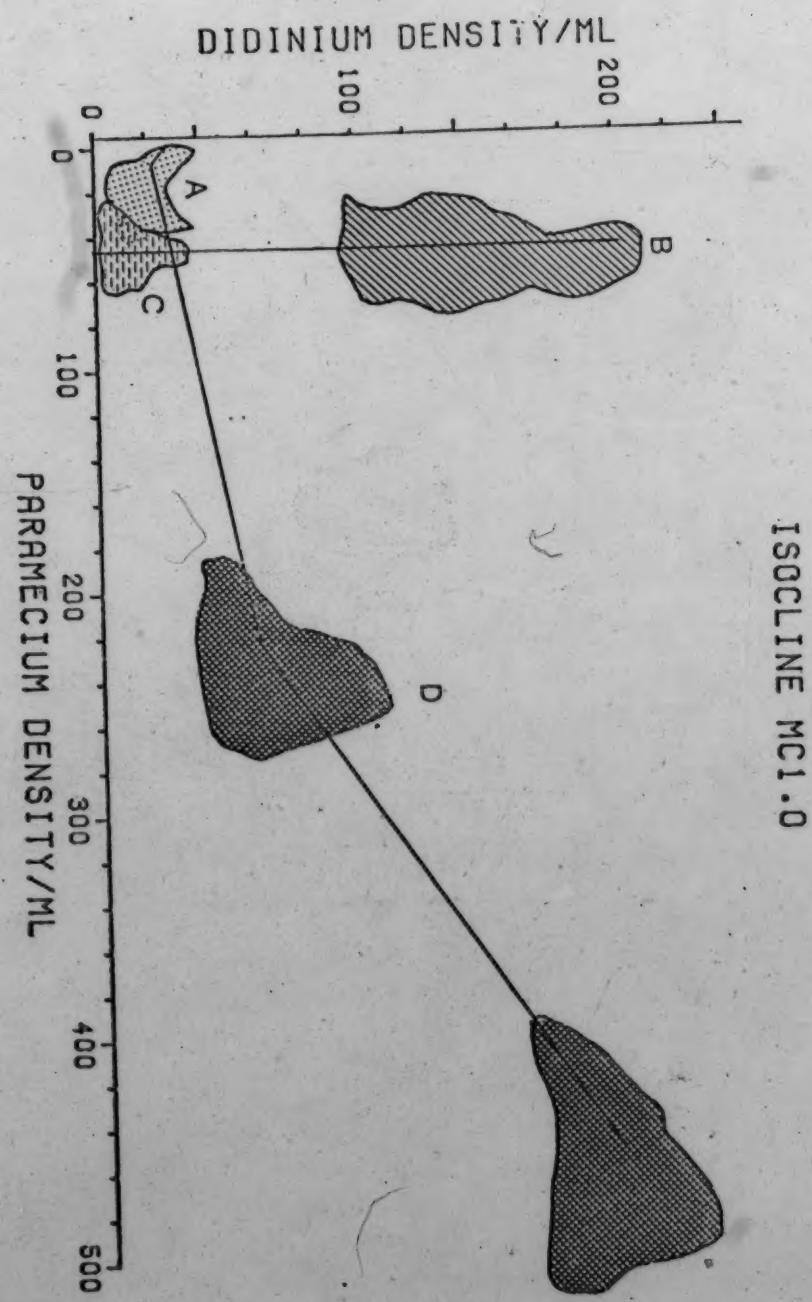

DIDINIUM DENSITY/ML
0
100
200
PARAMECIUM DENSITY/ML
0
100
200
300
400
500
A
B
C
D
ISOCLINE MC1.0

Figure 17b.

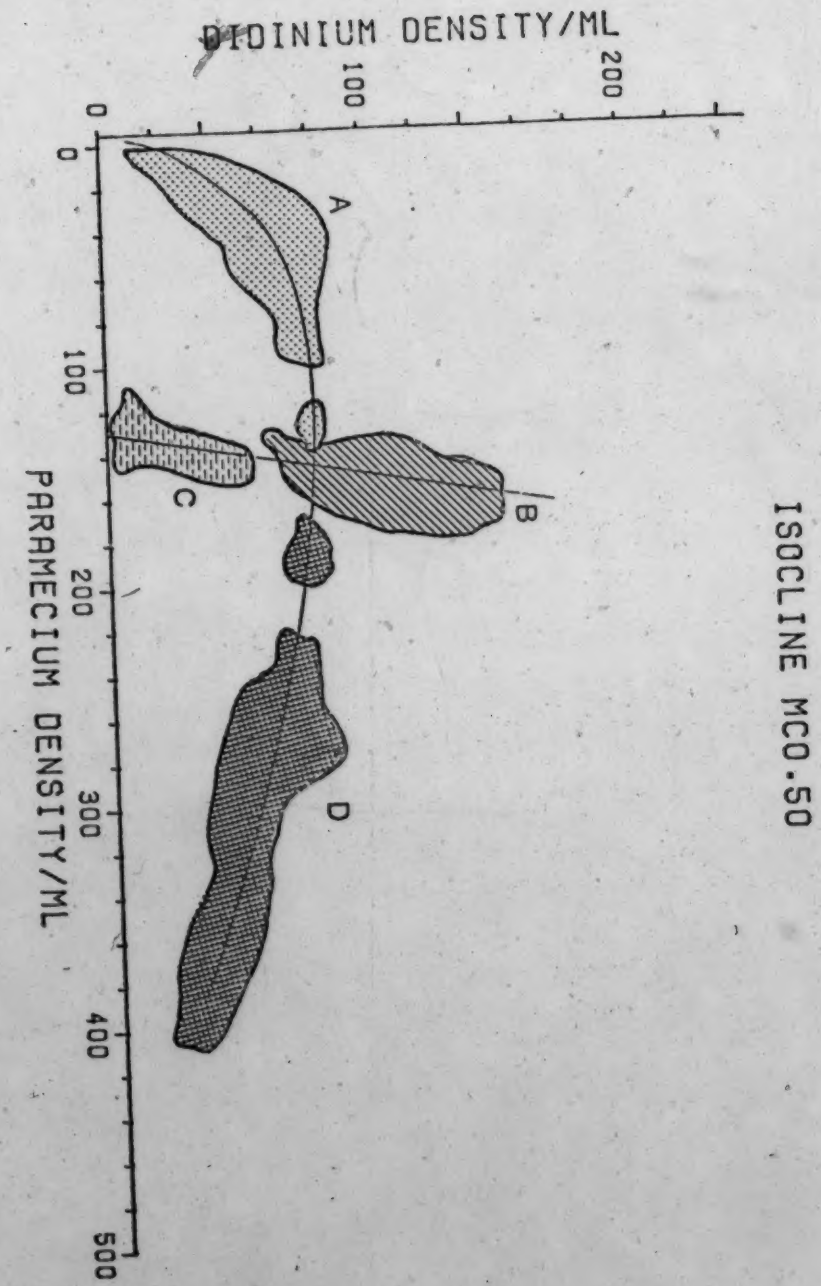

DIDINIUM DENSITY/ML
0
100
200
PARAMECIUM DENSITY/ML
0
100
200
300
400
500
A
B
C
D
ISOCLINE MCO.50

Figure 17c.

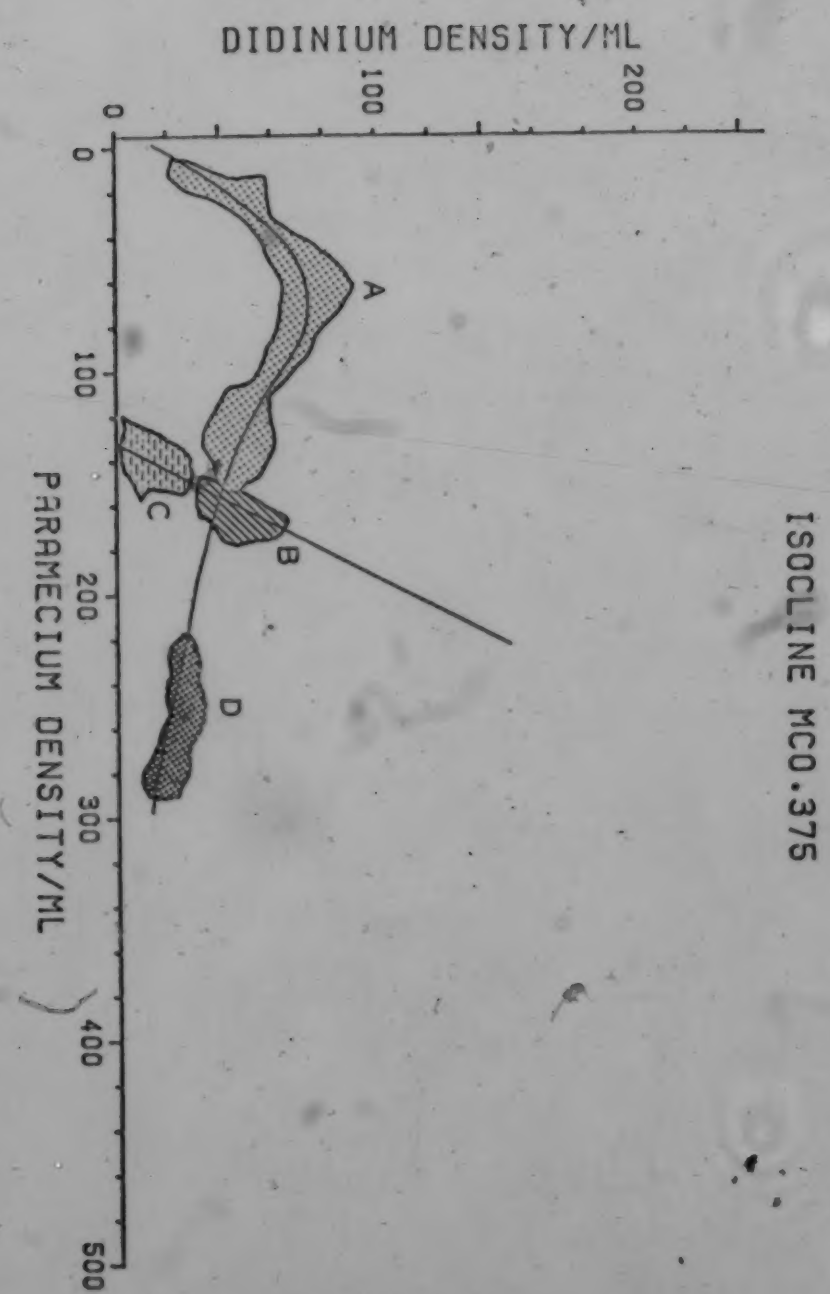
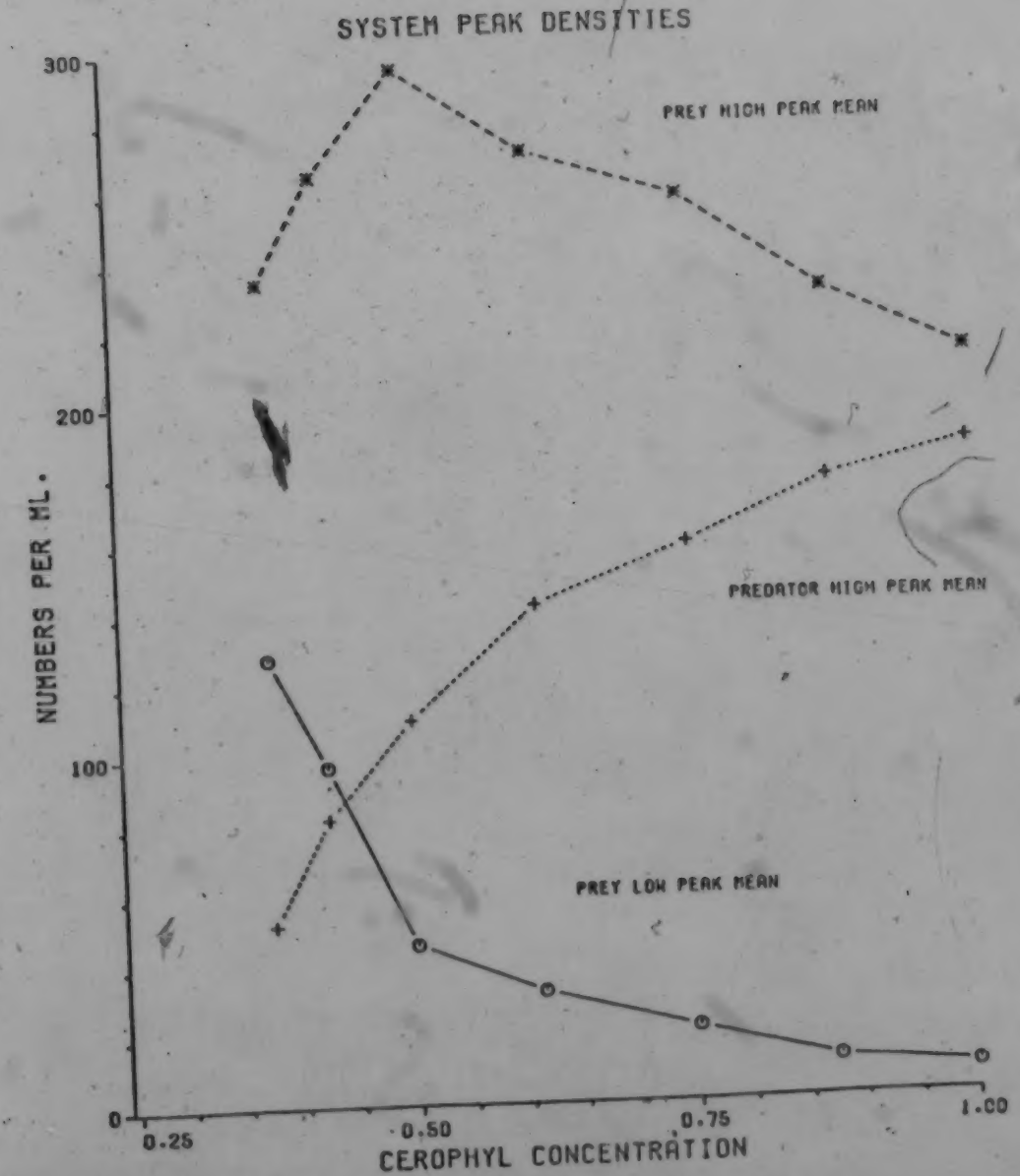

DIDINIUM DENSITY/ML
0
100
200
PARAMECIUM DENSITY/ML
0
100
200
300
400
500
A
B
C
D
ISOCLINE MCO.375

Figure 18.


SYSTEM PEAK DENSITIES
PREY HIGH PEAK MEAN
PREDATOR HIGH PEAK MEAN
PREY LOW PEAK MEAN
NUMBERS PER ML.
300
200
100
0
0.25
0.50
0.75
1.00
CEROPHYL CONCENTRATION